

Evolution of group living, and the importance of food and social organization in population regulation; a study on the red fox (*Vulpes vulpes*)

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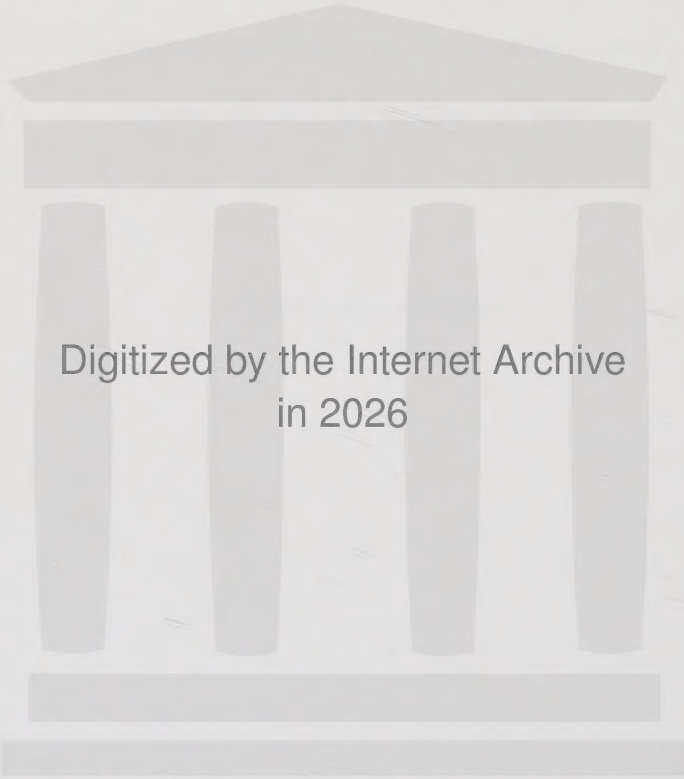
EVOLUTION OF GROUP LIVING, AND THE IMPORTANCE OF FOOD AND
SOCIAL ORGANIZATION IN POPULATION REGULATION;
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DISSERTATION

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LIST OF PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals.

- I Schantz, T. von. Spacing strategies, kin selection, and natural regulation of animal numbers. Manuscript.
- II Schantz, T. von. Prey consumption of a red fox population in southern Sweden. In: Zimen, E. (ed.). The red fox. Biogeographica; v. 18, Junk, The Hague, pp. 53-64. Reprinted by kind permission of Dr. W. Junk Publishers.
- III Lindström, E., Poulsen, O., and Schantz, T. von. Spacing of the red fox *Vulpes vulpes* (L) in relation to food supply. Manuscript.
- IV Schantz, T. von. 1981. Female cooperation, male competition, and dispersal in the red fox *Vulpes vulpes*. *Oikos* 37: 63-68. Reprinted by kind permission of *Oikos*.
- V Schantz, T. von. Red fox numbers, reproduction, and social organization at different prey densities. Manuscript.



PREFACE

When I began studying foxes as a postgraduate student in 1975, my main task was to investigate predation and competition by foxes in the Revinge area, south Sweden. This work was part of an integrated research project, concerning predator-prey relationships, under the guidance of Sam Erlinge at the Department of Zoology, University of Lund. At that time I made embarrassingly few visits to our library. Instead I spent most of my time in the field, mainly occupied with questions such as what are the foxes doing and when are they doing it? However, after having read the books by Dawkins¹ and Krebs and Davies², I enjoyed learning more about evolutionary theory and my visits to the library increased considerably in frequency. Now I mainly became concerned with questions such as why are the foxes behaving as they do? As the reader will find, the considerable proportion of this thesis is greatly influenced by my interest in evolutionary questions. Foxes, elusive as they are, are perhaps not the best suited objects for testing evolutionary theories since they furnish some difficulties in collecting adequate sample sizes. Accordingly, the generalizations presented below are based on a limited number of observations and data which can only reveal a small part of the complicated relationships between the fox and its environment. Still the foxes have furnished me with a lot of new ideas and I would be fully pleased if this thesis could be of value to a wider audience than pure fox specialists.

Various people helped me in my work. I am especially grateful to my supervisor Sam Erlinge, whose genuine interest and knowledge in carnivore ecology has been most helpful to me. Sam Erlinge and Per Brinck, Head of the Department, have always given me their full support when things did not go my way and showed great patience with me when I did not do things exactly as they wanted; for this I am very grateful. Sam also financed my field work by grants from the Swedish Natural Science Research Council and from the National Swedish Environment Protection Board. The warm and friendly atmosphere in the Wildlife Research Group stimulated me a lot in the development of different ideas on fox ecology, as did the cooperation with Erik Lindström at Grimsö Wildlife

¹Dawkins, R. 1976. The selfish gene. Oxford Univ. Press

²Krebs, J.R. and Davies, N.B. 1978. Behavioural ecology: An evolutionary approach. Blackwell, Oxford.

Research Station. I also thank Thomas Alerstam, Per Brinck, Pehr H. Enckell, Sam Erlinge, Lennart Hansson, Göran Högstedt, Hans Kristiansson, Hans Källander, Olle Liberg, Jon Loman, Ingvar Nilsson, Mikael Sandell, and John Veitch, who kindly offered helpful comments and criticism concerning the manuscripts. Considerable assistance in the field was given by Gunilla Andersson, Per Berglund, Catharina Cederlund, Jens Dahlgren, Claes Ericsson, Görgen Göransson, Sven-Olof Fransson, Sven Lundberg, Tom Nilsson, Birgitta Persson, Torsten von Schantz, Ulla Steinwall, Håkan Welff, and Anders Wetterin. All these peoples' enthusiasm and skill made lonely and often hard fieldwork a pleasure. Görgen Göransson constructed most of the radio transmitters and gave technical advice on the radio equipment, and his work is greatly appreciated. I am most grateful to Marianne Andersson's skillful help in the laboratory, and I express my thanks to Steffi Douwes, Gunilla Lindquist, and Ylva Zachrison, who drew the figures, typed the manuscripts, and arranged for the printing of this thesis. Last but not least, I want to thank my wife Ulrika, who endured my absence and presence, and who carried most of the burden. She also actualized the fitness concept by giving birth to Linn and Lycke. To these three the work is dedicated.

If all these prerequisites were sufficient for making sound science out of my work is for the reader to judge, but if you find it dissatisfactory, there is none to blame but myself.

BACKGROUND AND SUMMARY OF THE RESULTS

One of Darwin's main theories was that natural selection favours individuals who maximize their number of offspring in the next generation. With this background ecologists began to ask why is it so that populations seldom grow to such large densities that they overexploit their food resources and become extinct. Several different theories, dealing with e.g. food supply, diseases, climate, predation, and social behaviour were presented and "population regulation" became a classical topic in ecology. Field ecologists observed that when a population increased in density, the birth rate decreased, and several members of the population did not breed. This made, among others, Wynne-Edwards (1962) suggest that animals have evolved physiological and behavioural adaptations, e.g. low birth rates, to prevent overpopulation and that some individuals voluntarily avoided breeding for the good of the species or the population; i.e. group selection. However, Maynard Smith (1964, 1976) demonstrated mathematically that this theory does not hold true. In short, an individual who does not altruistically restrict its breeding effort but instead maximizes it (a "cheater") will, by Darwin's definition, be more fit, and hence outcompete the "altruistic" genotype. Even if a group selected population of altruists will be less likely to become extinct than a population of cheaters, it is likely that the altruist population, by e.g. immigration, will be invaded by the cheater genotype which is bound to spread through the population at the expense of the altruistic genotype. In 1964, two new basic concepts appeared in evolutionary theory; kin selection (Maynard Smith 1964) and inclusive fitness (Hamilton 1964). It had for long been recognized, that genes improving parental care would be selected for. However, parents and offspring are not the only individuals that carry genes in common but so do other relatives. Maynard Smith and Hamilton realized that the frequency of a gene in a population will be influenced not only by the effects that gene has on the survival and fertility of the individuals who carry it, but also by its effects on the survival and fertility of the relatives of that individual, i.e. kin selection, and, consequently, that the fitness of an individual depends both on its own survival and reproductive success and that of its relatives; i.e. inclusive fitness.

To survive and breed individuals have to cope both with the environment and with competition from conspecifics. In Paper I,

I present a partly new view on which strategies individuals living in fluctuating food environments theoretically should adopt to maximize their inclusive fitness. I also evaluate how such fundamental factors as food and kin selection can affect the population dynamics of vertebrates with parental care.

A fundamental aspect of theories on spacing strategies is that an animal should defend a territory when it is economically defendable (Brown 1964), i.e. if the net gain (in fitness) is greater when the animal is territorial than when it is not. As selection will favour those individuals whose strategy confers the greatest net gain, an animal will decrease its territory size, and thereby the cost of defense, when food supply is so high that the handling capacity (of food) is reached; i.e. the "just-sufficient" strategy. This view was challenged by Verner (1977) who suggested that an animal should defend a territory of a size larger than it needed. By this strategy the animals would prevent competitors from breeding and, thereby, increase the relative fitness of the "super-territory" holder. However, this theory was criticized since it was demonstrated that, unless the super-territory strategists derive some benefit from the resource surplus, such a strategy can not become stable in the population. Now, consider a territorial and permanently resident animal who lives in an interannually fluctuating food environment; e.g. the red fox in the Revinge area (Papers II, III, and V). If such an animal, instead of decreasing its territory size, maintains a fixed territory when food increases, it does not have to struggle for territorial enlargement later when food decreases; i.e. the "obstinate strategy" (Paper I). This view is supported by field data from central Sweden, where the foxes did not change their territory size although their main prey, voles, fluctuated markedly on a four year cycle (Paper III). Since an obstinate strategist during the "good" years maintains a territory that contains a resource surplus it faces the same "dilemma" as the super-territory strategist. However, as described in Paper I, the obstinate strategist can benefit from this resource surplus by allowing close relatives, e.g. earlier offspring, to remain as non-breeders in the territory to exploit the surplus. This simple model can be of general importance in explaining the evolution of group territoriality (Paper I).

Group living for the red fox is the main theme of Papers III, IV, and V. In accordance with the resource surplus view, it was

found that non-breeding group members mainly occurred during years of high food abundance (Papers III and V). It has been suggested that group living in birds and mammals may have evolved through kin selection by the non-breeders aid to the breeders (their relatives) in their reproductive efforts which hence would increase the reproductive success of the group, and thereby, increase the inclusive fitness of all the group members (e.g. Emlen 1978). This has apparently not been an important selective force in the evolution of group living for the red fox since radio-tracked non-breeding females did not seem to contribute substantially in providing food for the cubs (i.e. they visited the litters only occasionally) (Paper V), nor was the litter size larger during years when non-breeding group members were present than when hardly any non-breeders were present (Paper V). In fact, from the findings in Paper V it seems that if food is scarce the presence of non-breeders may reduce the breeding foxes' reproductive success, indicating that the breeders and the non-breeders competed for food. Competition is also implied by the data in Paper IV from which it appears that the breeding foxes mainly exploited rabbit habitats whereas non-breeders spent most of their time in vole habitats. In that way the non-breeders avoided competition with the breeding group members and so this probably increased the non-breeders' chances of remaining in the group.

The importance of unequal resource partitioning between members of the same population in maintaining population stability has been demonstrated in a theoretical model by Eomnicki (1980). In Paper I, I suggest that for a population of obstinate strategists the fluctuations in food density will be damped by the presence or absence of non-breeding group members. Such a population will be stable because the resource fraction canalized into reproduction will vary according to the variations in resource availability. In low years a high proportion of the available food resources will be utilized for reproduction due to the fact that most individuals present are breeders. As resources increase, so will group and population size. The resource intake will be unequally distributed between individuals in such way that the breeders utilize resources both for reproduction and maintenance, whereas the non-breeders only utilize resources for their maintenance. Thus, as food increases, the smaller the fraction of available resources that will be utilized for reproduction, and the lower the birth rate will be. This is partially supported by the results

in Paper II and V.

It appeared that during the "good" rabbit years (1975 and 1976) the foxes consumed only a small fraction (i.e. 11 %) of the annual production of rabbits which were, however, the most important prey for the foxes (Paper II). In 1977 the rabbit population decreased and the lowest densities were recorded 1980 and 1981. In spite of the variable rabbit density, the number of foxes in spring remained almost constant from 1975 through and including 1980. During these years fox groups consisting of breeders and non-breeders (Paper IV) were probably the predominant social unit (Paper V). In the spring of 1981, however, there were only half the number of foxes present in the study area compared with previous years, and in this year male-female pairs were probably the most common social units (Paper V). In 1981 the density of rabbits was very low, yet the number of fox cubs produced per adult fox was the highest ever recorded during the study, i.e. the number of fox cubs/adult in 1981 was 2.15 whereas the average figure between 1976 to 1980 was 1.28, S.D. = 0.58 (data from Paper V). Also the number of fox cubs produced per rabbit (as estimated from the relative spring densities of rabbits, Table 1 in Paper V) was highest in 1981; in 1981 1.08 fox cubs were produced per rabbit whereas the average figure between 1976 and 1980 was 0.46, S.D. = 0.18 (data from Paper V).

The foxes' numerical response to changes in rabbit density probably also included multiple breeding, i.e. at high rabbit densities more than one female per fox group bred (Paper V). Above a certain prey density, it may be profitable for the breeder if one of the non-breeding group members becomes a breeder, e.g. by territorial budding (Paper I). On the other hand, a drastic and sudden decrease in food supply could make such a strategy costly for the breeder, for whom the alternative to territorial budding would be to increase group size. The foxes probably did not respond by increasing group size at the end of the rabbit increase (during 1975 and 1976) since the number of foxes in spring remained almost constant for these two years (Paper V). The occurrence of multiple breeding mentioned above could have been an early stage of territorial budding (see also Paper III), and I believe that if the rabbit population had continued to increase in density this might have caused territorial budding with new independent groups being created. Now the rabbits instead decreased in density which made the multiple breeding strategy non-profitable. Accord-

ingly, as the rabbits continued to decrease only one female per group bred (Paper V).

In conclusion, it appears that the fox population in the Revinge area was ultimately regulated by food and proximately by their social organization. Food (Paper II) affects, among other things, the foxes' spacing strategy (Paper III). Food, spacing strategy, and kin selection are important factors in the evolution of group living (Paper IV). The interaction of all these factors influences the dynamics of the fox population (Paper V).

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SPACING STRATEGIES, KIN SELECTION, AND NATURAL

REGULATION OF ANIMAL NUMBERS

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ABSTRACT

This simple non-mathematical model predicts that non-migratory animals living in a cyclic environment would have a constant territory size if the environmental cycle is predictable, and if the animals' life span is longer than the cycle. An animal, which adjusts its territory size to the different resource levels in the environmental cycle (the "JS-strategy"), has to fight against conspecifics each time it has to enlarge its territory due to a resource decline. Conversely, this extra cost is avoided by an individual holding a permanent sized territory adjusted to its needs during the low years (the "obstinate" strategy). However, the latter strategy implies that during years of high resource abundance, the individual defends a territory that contains resources which exceed the owner's need for reproduction and maintenance. Therefore, the model predicts that the obstinate strategist would permit some of its offspring to remain in the territory to exploit the super-abundant resources. If an expected decline in resources occurs in the near future, then the animal would prevent its offspring from breeding. But if the resource decline is expected in the remote future (i.e. when the individual is already dead), and if the territory holder's own reproductive success is not affected, then the animal would allow its offspring to keep a smaller territory within the former larger one and breed there on its own. If the resources still remain super-abundant, additional "offspring territories" are expected to bud off. Thus, in the latter case, selection infallibly extorts JS-strategists. At high densities such a population is sensitive to changes in food supply and can not be stable. In contrast, a population of obstinate strategists is less sensitive to changes in food supply and is more likely to be stable. The presented model may give a new understanding of the adaptive significance of group living for birds and mammals. The model may also shed some light on vole population cycles.

INTRODUCTION

It is almost twenty years since Hamilton (1964) and Maynard Smith (1964) coined the terms "inclusive fitness" and "kin selection". Although these basic theoretical concepts have become cornerstones in recent behavioural theory, they are still rarely included in theories of population dynamics; one exception is Charnov and Fiererty (1980). As pointed out by e.g. Stearns (1976, 1977) and Eomnicki (1980), most models on population dynamics consider populations of phenotypically identical individuals having only age dependent differences in fecundity and survival. However, Chitty (1967) hypothesized (i) that the genetic composition of a vole population changes during a cycle; at high densities selection favours aggressive animals with low reproductive rates, and less aggressive animals with high reproductive rates at low densities, and (ii) that spacing (or aggression) is the variable which drives the machinery through the cycle. Although much recent work has focused on genetic changes during the population cycle of voles (e.g. Krebs and Myers, 1974), there is still only preliminary and suggestive evidence for genetic changes during a vole cycle (see e.g. references cited by Gaines and McClenagham, 1980, p. 178).

On the other hand there is no doubt that spacing behaviour, i.e. territoriality and dispersal, has an impact on population dynamics. Territoriality frequently prevents individuals from breeding or may force some of them to breed in suboptimal habitats (e.g. Brown and Orians, 1970; Watson and Moss, 1970; Krebs, 1971; Brown, 1975; Wilson, 1975). In many mammals (Bertram, 1978) and in some birds (Emlen, 1978), those individuals occupying a territory form a kinship-group, i.e. a group of adult individuals which are related to each other, and in which, most often, the individuals are organized in a rank order (e.g. Wilson, 1975). Usually only the highest ranked individuals breed (Watson and Moss, 1970; Brown, 1975; Wilson, 1975; Emlen, 1978; Woolfenden and Fitzpatrick, 1978). As aggression is the most important variable governing territoriality, dominance hierarchy and perhaps also dispersal, it is surprising that so little interest has been paid to behavioural aspects in theories of population dynamics (see also Watson and Moss, 1970; Brown, 1975). In this paper the interactions between spacing behaviour, kinship and population dynamics will be discussed.

Here I will develop a model for spacing and reproductive strategies (considering inhibition of reproduction through social mechanisms) of animals living in fluctuating environments. I will also evaluate the influence of these factors on population dynamics. In this analysis certain interest is paid to the importance of inclusive fitness and kin selection, because the degree of aggression and altruism between individuals (and thereby also spacing) probably depend on the genetic relatedness between them (Hamilton, 1964, 1971, 1972).

The model is restricted to vertebrates with parental care, i.e. where a kin recognition can be developed and where the clutch or litter size depends on the parents' ability to provide food for their young.

THEORY

TERRITORY SIZE AND KIN SELECTION

Contemporary theory predicts that territory size would expand as resources decline (e.g. Dill, 1978; Hixon, 1980). This is analogous to Brown's (1964) suggestion that an animal will hold a territory when it is "economically defendable", i.e. if the balance of the gains (in fitness) resulting from a more or less exclusive use

of an area and the costs (in fitness) of defence are such that the net gain is greater if the animal is territorial than if it is not (see also Carpenter and MacMillen, 1976). As selection will favour those individuals whose strategy results in the greatest net gain, an animal will decrease its territory size, and thereby the cost of defence, once food density is so high that the provisioning (handling) capacity is reached (the "just-sufficient" strategy).

On the other hand, an animal living in an interannually fluctuating environment, occupying its territory for several years (e.g. red fox (Vulpes vulpes), pers. obs.; tawny owl (Strix aluco), Southern, 1970), or throughout its whole reproductive life (e.g. Ural owl (Strix uralensis), Lundberg, 1979) is facing a different situation. If such an animal decreases its territory size in accord with increasing food resources and if the "empty" space between the shrinking territories is occupied by other individuals, then the animal has to fight against conspecifics each time resources decline, i.e. when it has to enlarge its territory. In contrast, an animal who does not decrease its territory size when food production increases can, since it does not have to fight for an enlargement, devote more energy to territory defence when food decreases. Hence, individuals adopting the latter strategy (the "obstinate" strategy) would be more fit during the low years, since they maintain an optimal territory size (containing an adequate food supply) more economically than the "just-sufficient" strategists (hereafter called JS-strategists).

However, during years of high resource abundance, JS-strategists benefit most since they defend smaller territories that contain just sufficient resources whereas obstinate strategists have territories that contain a resource surplus. Therefore, unless obstinate strategists derive some benefit from this resource surplus, such a strategy can not become stable in the population; see e.g. the discussion by Colgan (1979), Getty (1979), and Pleasants and Pleasants (1979) of Verner's (1977) super-territory model. However, such an extra benefit may be derived through kin selection: Maynard Smith (1964) defined kin selection as "the evolution of characteristics which favour the survival of close relatives of the affected individual". Such behaviour is selected for because it increases the individual's inclusive fitness (Hamilton, 1964). Consequently, in a mixed population an individual who allows its close relatives to exploit a resource surplus (i.e. resources not necessary for its own survival and reproduction) is

selected for, whereas an individual who allows non-relatives to exploit the resource surplus is selected against. The obstinate strategist will therefore gain by allowing some of its offspring (but probably not all of them; see Hamilton and May, 1977) to remain in the territory during years of high resource abundance. This will not only increase the survival rate of its offspring but probably also reduce the cost of territorial defence and perhaps even reduce the cost of raising young through the helper-effect (Emlen, 1978).

During a resource decline there is a cost associated with both strategies. JS-strategists have to fight against their non-related neighbours for a territory enlargement, while obstinate strategists have to expel their adult offspring. There are at least two reasons, one non-genetical and one genetical, to assume that, again, the latter strategy is less costly:

(i) Maynard Smith (1974b), Parker (1974), and Maynard Smith and Parker (1976) stressed the importance of asymmetry in settling contests without escalating; this is the non-genetical argument. They concluded that in symmetric contests, escalated conflicts will occur. In asymmetric contests, the asymmetry will be taken as a cue by which the contest can be settled conventionally without any fight. Hence, "in the absence of some asymmetric cue, the cost of contests, either in the risk of injury or in the cost in time and injury, is likely to be large" (Maynard Smith and Parker, 1976, p. 173). A contest between two animals which hold contiguous territories with the same RHP (resource holding potential; Maynard Smith and Parker, 1976) is probably symmetric, whereas a contest between an alpha and a beta individual in a dominance hierarchy most likely is asymmetric (e.g. Parker, 1974).

(ii) The genetical argument is that even the loser in a contest between related individuals gains some fitness through kin selection as the winner is his relative; no such "loser's reward" occurs if the combatants are unrelated (Fig. 1).

I hence conclude that in fluctuating environments, parents who allow some of its offspring to remain in their territory to exploit surplus resources in "good years" instead of reducing their territory, benefit in terms of inclusive fitness. In the next section I will show that this is only partly true.

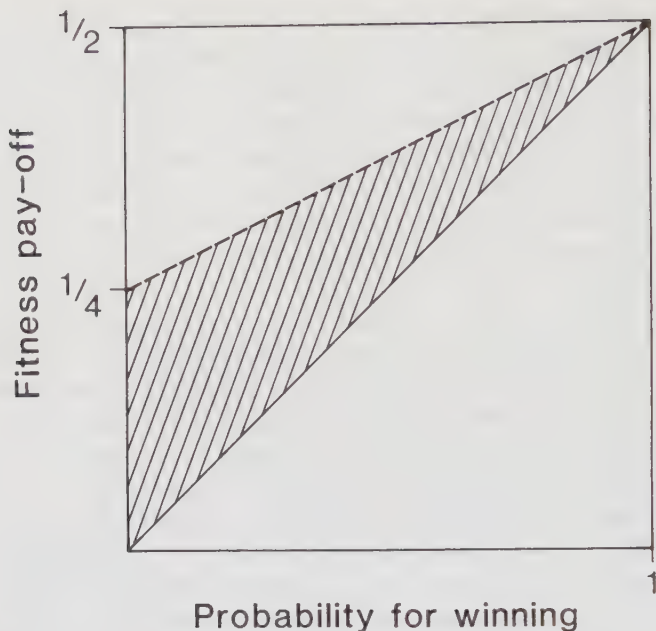


Fig. 1. A schematic representation of fitness pay-off as a function of the probability for an individual to win a territory contest against an unrelated combatant (lower solid line) and against a full sibling or an offspring (upper broken line). The fitness pay-off is measured as the coefficient of relatedness between the combatant and the offspring born in the territory after the contest. The hatched area denotes the space where the function is located at different coefficients of relatedness ($0-\frac{1}{4}$) between the combatants. Thus, at any given probability ($p < 1$) to win the contest, the individual always can expect to lose more in fitness if its combatant is genetically unrelated than it can if the coefficient of relatedness between the combatants is more than zero.

REPRODUCTION IN KINSHIP GROUPS

In this section I will discuss the importance of monopolizing reproductive opportunities in kinship-groups in relation to the predictability of environmental fluctuations and the animals' expected life span.

It is well-known that dominant individuals displace subordinates from food and breeding opportunities (Wilson, 1975). In fish, Borowsky (1978) showed that dominants inhibited the sexual maturation of subordinates. In wolves (*Canis lupus*) the alpha female obstruct copulations between subordinate individuals (Rabb et al.,

1967) or expels the mated subordinate female from the group (Peterson, 1979). In some cases the subordinated females' offspring are aborted or deserted (wolf, Altmann, 1974; dwarf mongoose (Helogale parvula), Rood, 1980; red fox, von Schantz, 1981) or even killed by the alpha female (African wild dog (Lyacon pictus), van Lawick, 1973). The mechanism may also be indirect, e.g. the alpha(s) exclude the subordinates from optimal habitats (von Schantz, 1981) or optimal feeding places (Murton et al., 1966) suggesting that the resources left for the subordinates are not enough for successful reproduction. Thus, dominants are in various ways capable of preventing subordinates from raising offspring. Under what circumstances should this power be used by the dominants?

A dominant individual should prevent its adult subordinate offspring (hereafter called beta individuals) from breeding when (i) the dominant itself can produce an optimal clutch or litter size adjusted to the food resources in the territory, and (ii) when competition from the beta individual's offspring will reduce the survival rate of the dominant's own offspring more than its gain in inclusive fitness. This is valid only on the assumption (which I make here) that inbreeding is selected against (see e.g. Ralls et al., 1979, and references cited there).

For simplicity, I assume that the alpha pair is the same in all breeding seasons. The coefficient of relatedness r (Hamilton, 1964) between the alphas and their outbred grandchildren is $1/4$. Therefore, the alphas should prevent their offspring from breeding as long as the conditions in point (i) are met. There is no obvious conflict here with the "interests" of the betas as r between them and the "new" offspring is $1/2$, the same as with own offspring.

The outcome is less obvious if the resource supply of the territory could sustain more than one litter. Presumably, breeding of related betas is the only stable strategy that can evolve in such a social system, because if any of the alphas took a new mate from outside, this would be negative to all the other members in the group, and one of the important benefits for the betas to remain at home would be eliminated, namely their role as "hopefully reproducers" (Emlen, 1978), i.e. a severe weakening of the selective advantage to remain as a beta. (This also implies that when one of the alphas dies we can expect a split of the family group due to the conflicting interests among the group members; see Emlen, 1978, pp. 262-263). The betas are the only individuals

in the group that carry genes shared with all group members ($r = 1/2$). Therefore, if the resource supply permits an extra litter the most likely individual to breed would be a beta. This, however, will lead to a new conflict, since the beta must select a new unrelated mate. An unrelated individual in the group potentially creates a cost to all the other members of the group since it would compete both for food and for a position in the dominance hierarchy, i.e. mating opportunities and future tenancy of the territory. Such competition will most probably reduce the inclusive fitness for all the "original" members, except for the individual with which the "stranger" actually mates. These costs are probably much reduced if the beta (which is about to breed) and its unrelated mate establish a smaller territory on their own within the former group territory; i.e. territorial budding. On the assumption that this beta dominates all the other beta individuals, all the group members will benefit from this strategy. The alphas will have grandchildren brought up on the resource surplus they could not use for their own reproduction. The beta will become an alpha (as will its new mate) and the other beta individuals will all gain one step in the hierarchy and become closer to an eventual alpha status.

However, even if it is favourable for the time being there are situations when the alphas still lose inclusive fitness by permitting territorial budding. Since the alphas lose priority of access to the resources in the budded territory, a sudden and drastic decrease in the resource supply could reduce the reproductive success of the alphas more than it would have done if budding had not occurred. More precisely, the alphas gain in inclusive fitness by territorial budding only when

$$P < P(1-R) + \frac{G(1-K)}{2} ,$$

where P is the alphas' expected future production of own offspring if budding had not occurred, G is the number of grandchildren produced in the budded territory during the rest of the alphas reproductive life, and R and K is the proportion of P and G , respectively, that succumb due to budding. R and K depend on the expected food shortage (occurring simultaneously in both territories) such that if no shortage occurs R and K is zero but will increase up to unit according to the rate of food shortage. If we assume that P is similar to G and that R is similar to K , then for

the alphas to gain from budding, R (and K) must be less than $1/3$. However, food shortage is likely to affect reproduction in the budded territory more strongly than the reproduction in the alphas' territory; thus $K > R$. It is also likely that G is less than P . Therefore, according to the inequality above most probably R should be even less than $1/3$ if budding should be profitable for the alphas. Hence, if a drastic decrease in food abundance is expected in a near future the alphas would do best in not permitting territorial budding.

If the resource decline is expected in a remote future, however, budding is likely to occur. Even if $R = 1$ at time $t + 1$, the number of offspring and grandchildren born up to and including time t when $R = 0$, can outnumber the loss from time $t + 1$ and onwards; P decreases with time due to an increased probability for the alphas of dying. Accordingly, at such circumstances we shall expect territory size to decrease in accord with increased food density; i.e. the JS-strategy.

POPULATION REGULATION

In a population of obstinate strategists the resource fraction canalized into reproduction will vary according to the variations in resource availability. In low years a great fraction of the available food resources will be utilized for reproduction during the breeding season due to the fact that most individuals present are breeders. As resources increase, so will group size and population size. The resource intake will be unequally distributed between individuals, such that the alphas (breeders) utilize resources both for reproduction and maintenance whereas the betas only utilize resources for their maintenance. Thus, unless the conditions for territorial budding are met, as resources increase, the fraction of available resources utilized for reproduction will decrease, and so will increase rate per individual. In fact this is what many ecologists (e.g. Nicholson, 1933; Wynne-Edwards, 1962) would have called density dependent reproductive rate or population self-regulation.

In contrast, in a population of JS-strategists the resources will be more equally shared between individuals and the majority of the food taken will be canalized into reproduction, irrespective of food abundance; in all years most of the resident individuals are breeders. Therefore, there will be a close relationship

between resource availability and the rate of population increase. During a resource increase there will be a corresponding increase in population size; larger than that of a population of obstinate strategists. When the resources decline, a resource shortage for the majority of individuals can be expected with decreased overall reproductive rate, large emigration rate, heavy mortality, and, consequently a drastic decrease in population size. Hence, a population of JS-strategists will show marked oscillations in size and rate of increase according to the variations in resource supply.

The importance of unequal resource partitioning between members of the same population for maintaining population stability has been demonstrated in a mathematical model by Komnicki (1980). The model suggested that unequal resource partitioning between the members of the population, e.g. due to different positions in a social hierarchy, is necessary for population stability, whereas equal resource partitioning causes instability.

The importance for population stability, of individual partitioning of the resources and the effectiveness of their conversion into reproduction, perhaps become clearer if we consider the hypothetical model in Fig. 2. Here I have considered two types of birds; Type I lives as a single breeder in a large territory (with the area A) whereas Type II lives, also as a single breeder, in a small territory (with the area $a = \frac{A}{9}$). The birds are supplied with a given number of food items e.g. worms; in case (i) there are 90 worms per A, thus 10 per a, in case (ii) there are 45 worms per A, thus 5 per a, and in case (iii) there are 36 worms per A, thus 4 per a. It is assumed that it takes t time units for the birds to clear the area a from all worms, consequently it takes 9t time units for the Type I bird to clear area A from all worms. The birds are allowed to search for worms during T time units, such that $t < T < 9t$. During T time units, each bird needs 5 worms for maintenance, the rest of the worms taken are converted into reproduction and thus analogous to rate of increase (RI in Fig. 2).

In all the cases (i, ii, and iii), the Type I bird has a greater reproductive output than each of the Type II birds. However, at the highest worm density (case i), within the given area, the Type II birds together have a greater rate of increase than that of the Type I bird. This latter outcome is a consequence of equal resource partitioning between the Type II birds and thereby their overall greater efficiency of converting the available resources

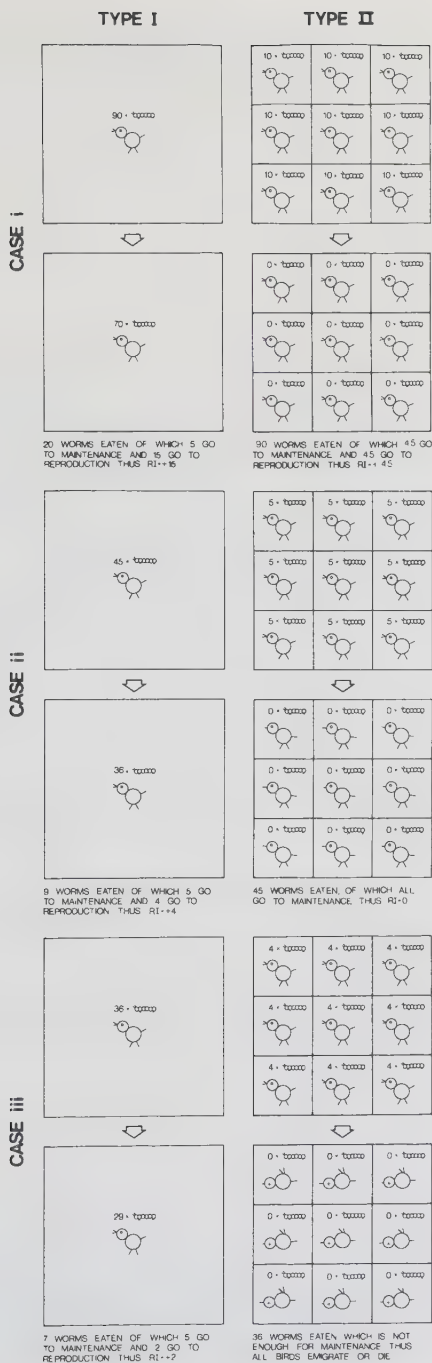


Fig. 2. A schematic presentation of population rate of increase in relation to spacing strategies and food abundance. In each case (i, ii, and iii) both types of birds are supplied with the same number of food items (worms) per unit area. The upper figures in each case show how many worms the birds are supplied with. The lower figures in each case show how many worms that are left after T time units. RI symbolize the "population" rate of increase within the given large box. For further explanations see the text.

into reproduction. Fig. 2 also shows that a population of Type II birds is more sensitive to changes in food supply than is a population of Type I birds confined to an accordant change; again this is due to the equal resource partitioning between Type II birds, and, thus, in accordance with Komnicki's (1980) model.

PREDICTIONS

The following main predictions can now be made:

(i) In a population that is confined to a cyclic or otherwise predictably fluctuating environment where the animals' life span is longer than the cycle we shall expect neither an increase in the number of breeding individuals nor a change in territory size during resource increase. Instead, the number of resident non-breeding beta individuals shall be expected to fluctuate in parallel with the resource cycle. Thus, we can expect a regulated population where the resource fluctuations are buffered through the presence or absence of non-breeding beta individuals.

(ii) If the animals' life span is shorter than the environmental cycle we shall expect an increasing number of breeding animals during the log phase of the cycle due to territorial budding. Non-breeding individuals will occur at the end of the log phase and during the peak. During the resource decline there will be frequent symmetrical contests for territorial enlargement. Since such contests most likely are costly (Maynard Smith and Parker, 1976) we can expect a severe reduction both in the number of breeding individuals (alphas) and in breeding success for those that still manage to breed. In this system, selection favours JS-strategists; as a consequence, there will be marked population oscillations related to the environmental cycle.

EVALUATIONS OF PREDICTIONS

DOES TERRITORY SIZE VARY IN RELATION TO FOOD AVAILABILITY?

An inverse correlation between territory size and food density has been observed in many birds (e.g. Kluyver and Tinbergen, 1953; Lockie, 1955; Pitelka et al., 1955; Stenger, 1958; Schoener, 1968; Holmes, 1970; Maher, 1970; Cody and Cody, 1972; Newton et al.,

1977). However, since all these studies concern birds that are migratory or territorial only during the breeding season, they do not contradict the present model. Such species most likely would be JS-strategists since they must reestablish their territories each breeding season. Therefore, they can not take any future advantage of keeping a territory larger than that necessary during a particular season, as they must fight against conspecifics over the territory borders at each establishment no matter the demarcation of the year before. However, some studies on the great tit (Parus major) (Lack, 1954, 1968a; Krebs, 1971) have indicated that year to year variation in territory size was not correlated with fluctuations in food supply in the breeding season. A possible reason for this was suggested by Maynard Smith (1974a) and Knapton and Krebs (1974) who showed that synchronous settlement of birds on their territories could result in twice the final density compared to asynchronous settlement. Another view was presented by Hildén (1965) who suggested that animals may respond indirectly to food, but directly to habitat type and adjust territory size to fit expected longterm mean expected prey density within a habitat type rather than responding to immediate prey density. This seems to apply to birds which establish their territories long before the factors influencing breeding success, e.g. food supply, are observable (Hildén, 1965; Seastedt and MacLean, 1979).

Studies on non-migratory animals show that territory size generally does not fluctuate with short-term changes in food supply (changes lasting for a shorter period than the animals' expected life span), thus supporting prediction (i) above (p. 22). This was shown for: (1) The rufous-sided towhee (Pipilo erythrophthalmus montanus), an insectivorous, permanently resident bird of chaparral in Arizona; they did not change territory size when being experimentally provided with extra food (Franzblau and Collins, 1980). (2) The acorn woodpecker (Melanerpes formicivorus) in California, a cooperative breeder in which a group occupies the same territory for years but one in which the food supply varies markedly from year to year (MacRoberts and MacRoberts, 1976). They pointed out (p. 45) that "it was only in situations of total acorn failure or when the crop was very poor that groups moved or expanded their territories. We observed no instance of a group reducing the size of their territory in response to an abundant acorn crop". Furthermore, (p. 43) "the area defended is larger than the area in use at any one period of time. In one year the woodpeckers may

use only a portion of the territory extensively, and in the following year different areas may become important because of variation in acorn production, insect abundance, and other factors. Areas not in use are defended and may become important later".

(3) Neither Southern (1970) nor Lundberg (1979) found any change in territory size or number of resident pairs in the non-migratory tawny and Ural owls, respectively, although their main prey, small rodents, fluctuated markedly on a 3 - 5 year cycle.

(4) Lindström et al. (in manus) did not find any change in territory size of the red fox in central Sweden where the rodents have a 3 - 4 year cycle.

Davies (1978) suggested that one reason why the tawny owl density in Southern's (1970) study remained so stable was that there is little variability in the settlement pattern; owls are long-lived birds, and territorial boundaries remain almost exactly the same from year to year. However, also the great horned owl (Bubo virginianus) is a relatively long-lived bird, (Mean annual mortality rates of great horned owls were found to be 55 % in the first year of life, 39 % in the second, and 22 % thereafter (Adamcik et al., 1978).) which remains on its territory throughout the year (Baumgartner, 1939). Yet, the number of territorial pairs of this owl increased three times during the increase phase of the snowshoe hare's "10-year-cycle" (Keith et al., 1977). Unfortunately, Keith et al. (1977) did not present data on whether this increase in territorial pairs was due to decreased territory size (e.g. by territorial budding) or due to settlements of immigrants in unoccupied areas.

IS HELPING AT THE NEST THE CAUSE OF GROUP LIVING?

Typical of group breeders studied to date is close genetic relatedness between the breeders and the non-breeding betas, or helpers, in each group. The different benefits to animals living in kinship-groups have been reviewed by Bertram (1978) and Emlen (1978). Bertram (1978) concluded that one advantage of pack-hunting to predators is their greater ability to catch large prey. But not all cooperatively breeding, or group living, animals hunt cooperatively. The evolution of cooperative breeding in birds is a matter of controversy. Until recently, observations that birds with more helpers produced more young than birds with fewer or no

helpers (Emlen, 1978, Table 9.2) was thought to explain the evolution of cooperative breeding in birds (Lack, 1968b, Maynard Smith and Ridpath, 1972). However, Brown and Balda (1977) pointed out that none of these studies have assessed the impact of territory quality on reproductive success (Högestedt, 1980) or group size. By showing that group size in Hall's babbler (Pomatostomus halli) was positively correlated with territory quality (earlier also indicated by e.g. Zahavi, 1974, and Gaston, 1976), Brown and Balda (1977) questioned the prevailing ideas that avian helpers significantly raise the fitness of those whom they help, and thereby also the role of kin selection in the evolution of avian communal breeding systems.

Examples of other observations that do not fit the theory that communal breeding in birds primarily has evolved through the greater reproductive success in these groups (hereafter called the helper theory) are reports of birds being incompetent in their helping attempts, and of parents aggressively chasing such helpers from the nest (Emlen, 1978, p. 251). Zahavi (1974) even suggested that helpers in flocks of Arabian babblers (Turdoides squamiceps) were no help at all, and did more harm than good to their parents by getting in the way, attracting predators to the nest, and competing for food. Zahavi (1974) also showed that large groups did not generally raise more young than smaller groups (see also e.g. Woolfenden, 1975, Table 2). Moreover, in Florida scrub jay (Aphe-locoma coerulescens coerulescens), Stallcup and Woolfenden (1978) showed that many helpers (mainly females), although they were accepted in the group, made only minimal food contributions to dependent young. All these findings indicate that the helper effect was not generally the prime cause of the evolution of avian communal breeding systems. In addition, one might argue that if the helper theory is true we should expect a greater number of helpers in poor territories or during years of low food abundance and more active helpers as well (Gaston, 1978); at least the former prediction is not born out in most studies on cooperatively breeding birds, e.g. Zahavi (1974) and Brown and Balda (1977) (but see Reyer, 1980).

According to the theory presented in this paper, i.e. that the presence of helpers or betas is a consequence of resource surplus within the territory, I suggest that helping at the nest is a consequence of group living rather than the cause of it. A critical test of the resource surplus theory would be to manipulate

the food resources within territories of cooperatively breeding birds to see whether the group size responds to these manipulations or if instead there will be a change in territory size. I know of no such study, although e.g. the acorn woodpecker with its social plasticity (Stacey and Bock, 1978) seems to be a good candidate for such a study. In this bird, acorns and other nuts are collectively harvested by the groups in the autumn and stored in holes which usually are concentrated in one or two trees on the group's territory. The stored mast forms an important food resource during the winter (Stacey and Bock, 1978). These storage trees would be eminent objects for manipulating the food resources within each territory.

DOES GROUP SIZE VARY IN RELATION TO FOOD AVAILABILITY?

In an area where the production of acorns was extremely variable, acorn woodpeckers shifted between different spacing strategies according to the local abundance of food resources (Stacey and Bock, 1978). Those birds whose territories did not contain storage trees abandoned their summer territories by late autumn and early winter and migrated from the study area. In the spring, birds returned and established new territories. These birds did not breed in communal groups but in male-female pairs. Five groups of two to four adults remained on their territories throughout the winter. In contrast to the migratory birds, all of these resident groups had large storage trees or other mast storage facilities. In addition, three of these five groups also obtained food from artificial food sources. Some of the juveniles fledged by these latter groups remained on their natal territories during the winter. When birds depleted their acorn stores it was often the juveniles that left first (Stacey and Bock, 1978, p. 1299, see also MacRoberts and MacRoberts, 1976).

In another area (in New Mexico), with great fluctuations in the early production of acorns, the social groups of acorn woodpeckers were small and unstable (Stacey, 1979). This sometimes led to open reproductive positions (i.e. when an individual could join a group and become the only breeding member of its sex present in that group; Stacey, 1979, p. 1157) in some groups, whereas in some cases the whole group left their territory which then became unoccupied during winter. Groups on territories with more

storage facilities were more likely to have stored enough acorns to last through the winter to the start of the next breeding season, and were also more likely to have remained on their territories over the winter (cf. Stacey and Bock, 1978). Stacey (1979) also concluded that there was a significant correlation between the size of the group and the amount of storage facilities present on its territory (see also MacRoberts and MacRoberts, 1976). In spite of these findings, Stacey (1979, pp. 1163-1164) rejected the view that group size was dependent on food abundance; although, in my opinion, without convincing evidence. He motivated his conclusion by pointing out that the reproductive rate (number of young fledged per group per year) was greater among the small and unstable groups in New Mexico as compared with that of larger and more stable groups of acorn woodpeckers in California (studied by MacRoberts and MacRoberts, 1976); an area with less variable acorn production. (Note that this seems to contradict the helper theory.) Thus, according to Stacey food was not less abundant in the former population. However, since acorn woodpeckers feed primarily on insect and sap, and are not dependent on acorns, during the breeding season (Stacey, 1979, p. 1156, see also MacRoberts and MacRoberts, 1976), the comparison is, in this context, of no value. Nevertheless, Stacey suggested that a lower level of habitat saturation (see below), and not less abundant resources, was the primary factor that led to the low average size of the groups in New Mexico.

Selander (1964, cited by Emlen, 1978, p. 250) suggested that habitat saturation might favour the evolution of group living and cooperative breeding; due to low availability of unoccupied territories, suitable habitats become filled, and a portion of the population remain on their natal territories as non-breeders (see also Brown, 1974). This view is not exclusive to the resource surplus theory; in fact they are complementary. If there are unoccupied territories nearby the parental territory, both the breeder and the non-breeder are likely to gain in inclusive fitness by the latter's emigration and subsequent breeding (but see Emlen, 1978, pp. 255-260). At such circumstances, kinship-groups are not likely to develop until the unoccupied territories (habitats) become saturated.

Besides the acorn woodpecker, also many of the New World jays of North America, both the communal and the pair breeders, rely on insects and smaller vertebrates during summer while they often

feed on acorns and nuts during the mast crop season (Goodwin, 1976). Acorns and nuts are stored and utilized during winter (Goodwin, 1976; but see Brown, 1963). Although the acorn production is highly variable from year to year (see references cited by Stacey and Bock, 1978, p. 1299) the territorial system of the populations of cooperative breeders studied tend to be very stable with hardly any change in numbers of territories in each of the studied populations (Brown, 1974, Woolfenden, 1975; MacRoberts and MacRoberts, 1976; Stacey, 1979; but see Woolfenden and Fitzpatrick, 1978). However, the percentage of groups with helpers and the size of a given group tend to vary from year to year (e.g. Woolfenden, 1975; MacRoberts and MacRoberts, 1976, Appendix II).

In coyotes (Canis latrans), an essentially solitarily hunting carnivore which sometimes live in kinship-groups, winter weather influences the social behaviour (Bekoff and Wells, 1980). In years of increased availability of rodents (due to absence of snow-cover), juvenile coyotes remained in their native group sharing at least a part of their parents' territory; if the pups remained in association with their parents throughout their first winter, there was a good chance that they would remain through the following summer and perhaps beyond.

The red fox is another solitarily hunting carnivore which in some areas live in kinship-groups (e.g. Macdonald, 1979). In central Sweden where the voles fluctuate on a three to four year cycle, Lindström et al. (in manus) found that during vole peak years the foxes responded not by a decrease in territory size but by an increase in group size.

The robustness of the basic model is also indicated by Davies and Houston (1981) who demonstrated that pied wagtails (Motacilla alba) accepted subordinate wagtails in their winter feeding territories on days of high food abundance. By this strategy the territory owner gained help from the subordinate wagtail in territorial defence, which implied that the owner could maintain a fixed territory size. On days of low food abundance the territory owner evicted the subordinate from the territory.

Thus, there are several studies indicating that group size vary with food abundance. However, an important anomaly to the model is the fact that e.g. neither the tawny owl nor the Ural owl in Southern's (1970) and Lundberg's (1979) studies seem to retain their offspring in the territories during vole peak years. Although young owls, unlike most other birds, stay for a long

period in the care of their parents (Lack, 1968a), there is a high juvenile starvation mortality during autumn and winter in e.g. the tawny owl (Southern, 1970). Thus, in birds that do not cache food, it might be that, although food is plentiful, severe winter conditions, e.g. snowcover (cf. Bekoff and Wells, 1980), make food less available for the birds which then will cause a detrimental intra-specific competition if more than only a few individuals (the breeding pair) were present in the territory.

TERRITORIAL BUDDING

Recently it has been shown that within a kinship-group the earlier non-breeding subordinates inherit the territory and the breeding position from the alphas (e.g. lion (Panthera leo), Bertram, 1975; Florida scrub jay, Woolfenden and Fitzpatrick, 1978; wolf, Fritts and Mech, in press). A few studies have reported on territorial budding in the sense outlined above (pp. 17-19).

In tree squirrels (Tamiasciurus) that occupied non-overlapping territories throughout the year, breeding females just before weaning moved their young to nests at the edge of the female's original territory (in one case the female herself moved to a new territory) (Smith, 1968). The females then left a part of their original territories to their offspring which began to defend the budded territory on their own. In each family the mother kept the most productive trees and the best cache areas for herself.

Territorial budding has also been observed in the Florida scrub jay (Woolfenden and Fitzpatrick, 1978). Budding occurs when a helper male along with a prospective mate from outside his own family, takes possession of a segment of the male's natal territory. Typically the non-breeding male jay involved in this budding had dominated all other helpers in his family.

In the wolf new packs were often formed at the edge of parental territories (Fritts and Mech, in press); often a previously non-breeding pack member settled at the edge of the natal pack territory and mated there with another lone wolf. As a consequence of this, the parental territory often decreased in size. Fritts and Mech (in press) concluded that, breeding pack members might be more tolerant of their own progeny attempting to colonize at the edge of their territory than of unrelated wolves, so long as food is abundant.

None of these studies, however, can be taken as corroborations of the model on territorial budding (p. 18), since it is neither clear whether a period of food increase, that could not be matched by an increased reproductive effort of the original breeders, preceded the budding, nor is the age, i.e. expected future P in the equation (p. 18), of the original breeders known. In the Florida scrub jay case, budding appeared to occur only after territorial expansion; as the group grew, the territory expanded into adjacent territories occupied by smaller groups (Woolfenden and Fitzpatrick, 1978). Although this territorial expansion might be analogous to a resource increase, it is not strictly applicable to the model presented here.

ARE POPULATIONS OF OBSTINATE STRATEGISTS MORE STABLE THAN THOSE OF JS-STRATEGISTS?

The model in Fig. 2 is purely artificial, but it is supported by field data from a long-term study on great tits in Marley Wood at Oxford (Lack, 1968a; Perrins, 1979; and references cited by these authors). The great tit in England is non-migratory, during autumn and winter they often live in flocks (flocks normally range over the same area throughout the winter) (Krebs, 1971). During late winter, pairs which have been feeding in flocks gradually settle in a restricted area. At first the home range of a pair is not defended against other pairs. There is a gradual transition from home range to territory as defence of the area increases (Krebs, 1971). Lack (1968a) pointed out that in Marley Wood, the year to year fluctuations in territory size was not related to subsequent availability of food for the young. Krebs's (1971) feeding experiments indicated that territory size was not related to winter food supply. However, there was a positive relation between winter population size and subsequent breeding population size in Marley Wood (Krebs, 1971) (cf. Fig. 3A) which stresses the importance of synchronous settling and the pressure from potential settlers in determining territory size (breeding density is inversely related to territory size; Krebs, 1971). Gibb (1958, 1960) and Askenmo et al. (1977) have shown that tits during winter consume appreciable portions of arthropods and that they in some cases are capable of depleting their prey. This is supported by Fig. 3B showing that in Marley Wood there was a significant negative correlation

between winter population size of great tits and the density of caterpillars (important prey during the nestling period; Perrins, 1979) in the subsequent spring. Thus, a dense winter population of great tits resulted in both a dense breeding population and few available caterpillars subsequent spring. Fig. 3C shows that the mean number of young flying per pair was negatively correlated to number of breeding adults. Fig. 3D shows that there was a positive relationship between average number of fledglings per pair and caterpillar density. Thus, in general each breeder produced more fledglings if its territory was large and contained a great number of caterpillars than did a breeder in a territory with less food. This is analogous to greater reproductive output of the Type I bird than that of Type II bird in Fig. 2. In Fig. 3C, the Type I bird would be to the left on the horizontal axis (large territory and high reproductive output; cf. Fig. 2) and the Type II bird to the right (small territory and low reproductive output). In Fig. 3D, the Type I bird would be to the right on the resource axis (many worms) and the Type II bird to the left (few worms). Now if we look at the population level, there was a positive correlation between the total number of fledglings in the whole Marley Wood and the number of breeding adults (Fig. 3E) (see also Lack, 1964). Again this supports the model in Fig. 2 (case i), showing that in spite of the low individual reproductive output of Type II birds together they have a larger reproductive output (RI in Fig. 2) per unit area than have the Type I bird. At high breeding densities the great tits were more efficient in converting available resources (caterpillars) into reproduction (total number of fledglings) than at low breeding densities as indicated by the positive correlation between total number of flying young divided by density of caterpillars (an index of the efficiency by which the available resources are utilized for reproduction) and the number of breeding adults (Fig. 3G). There was no relationship between food density (number of caterpillars) and total production of fledglings (Fig. 3F). The results are in agreement with the model in Fig. 2. Namely that if a given area is fine grained into N small territories each of which is occupied by one breeder for which it takes t time units to find all available food items, then it will theoretically take t time units to convert all the available resources within the given area into reproduction and maintenance. Whereas if we within the given area only have one large territory occupied by one breeder it will take Nt time units

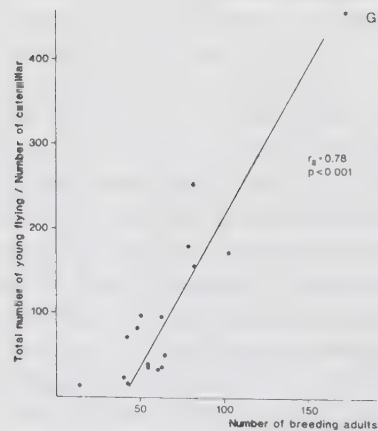
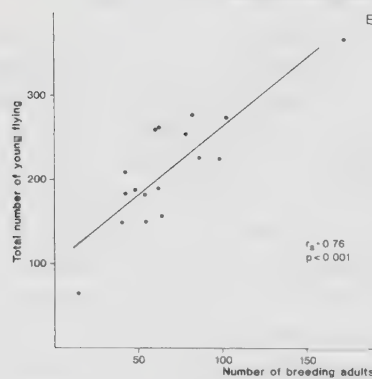
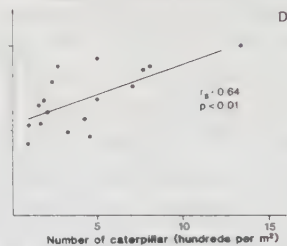
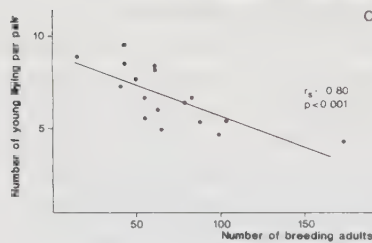
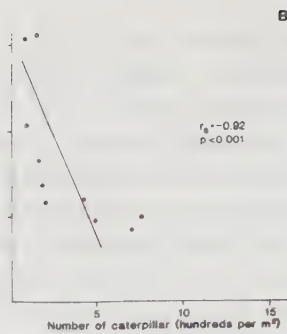
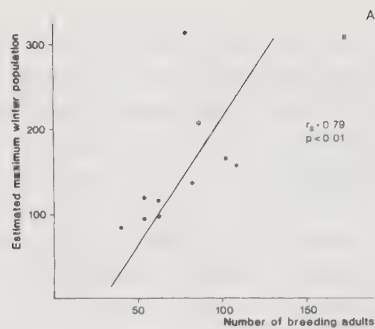


Fig. 3. Population changes of great tit in Marley Wood during 1947-1963. Data on population size and number of fledglings are from Lack (1968a, Table 11), data on caterpillar density are from Perrins (1979, Fig. 63). A regression line is denoted when the correlation coefficient (r) was significant ($p < 0.02$). Note that maximum winter populations was not estimated in all years. Therefore, correlations A and B are based on fewer points than the other correlations.

- A. Relationship between estimated maximum winter population and the number of breeding adults subsequent spring.
- B. Relationship between estimated maximum winter population and the density of caterpillars subsequent spring.
- C. Relationship between number of fledglings per pair and the number of breeding adults.
- D. Relationship between the number of fledglings per pair and the density of caterpillars. Note that Perrins (e.g. 1979, p. 199) rejected the idea that clutch-size in great tits was positively correlated to density of caterpillars (Lack, 1955). Perrins (1979) claimed that the apparent correlation was largely due to the fact that in 1948 there were large numbers of caterpillars and in 1951 very few; the clutch-size of great tits was the highest recorded in 1948 and the lowest in 1951. But, according to Perrins (1979), the variation in clutch-size in 1948 and 1951 can be explained in relation to other factors. I have not compared clutch-size with caterpillar density in the present analysis but only number of fledglings per pair. However, even if I exclude the data from 1948 and 1951 in all the comparisons in this figure, r_s will still be significant ($p < 0.05$) in all cases. In fact, it is only in correlation F below that r_s will change significantly; without data from 1948 and 1951, r_s will be -0.45 which means that $p < 0.05$.
- E. Relationship between total number of fledglings in the whole Marley Wood population and the number of breeding adults.
- F. Relationship between total number of fledglings in the whole Marley Wood population and density of caterpillars.
- G. Relationship between the conversion of fledglings from caterpillars and the number of breeding adults.

to convert all the available resources into reproduction and maintenance. Thus, unless the birds have Nt time units at their disposal, at any given food density, a dense population will utilize the available food more efficiently than would a less dense population. (But note that at high densities, each individual will probably have a lower fitness than at low densities.) Furthermore, if all individuals in the population breed, which essentially implies that there is no individual differences in resource intake in the sense of Bomnicki (1980), the population rate of increase (which can be both positive and negative) will be larger at any given food density than if only a fraction of the individuals breed. Bomnicki's (1980) model has demonstrated theoretically that the former population can not be stable whereas Fig. 2 indicates that a population which utilize only a fraction of the available resources for reproduction (which is analogous to presence of non-breeders) is less sensitive to changes in food density.

Now consider a contiguity of populations where at the left we have non-territorial animals, i.e. those that depend on resources that are not economically defendable in the sense of Brown (1964), e.g. many grazing ungulates (Owen-Smith, 1977), in the middle of the contiguity we have JS-strategists, e.g. many migratory birds and short-lived animals that are confined to a fluctuating food resource. At the right extreme we have obstinate strategists, i.e. those that by kin selection are capable of monopolizing the breeding rights within a permanent territory and thereby maximizing their fitness, e.g. many group living birds and mammals. If the views above are generally true, then we should expect that different populations of the same species, with the same innate capacity for increase, scattered over the whole contiguity should respond to a similar resource change in the following way:

$$\left| \frac{d\bar{N}_{\text{left}}}{dt} \right| > \left| \frac{d\bar{N}_{\text{middle}}}{dt} \right| > \left| \frac{d\bar{N}_{\text{right}}}{dt} \right| .$$

Unfortunately, I know of no species that covers the whole contiguity. Therefore, I can only relate this prediction to different species.

Seasonally migratory ungulates are generally non-territorial (e.g. Owen-Smith, 1977). Pimlott (1967) stated that deer, caribou, moose, and sheep, which are non-territorial, appear to have no self-regulation of their numbers (see also Tanner, 1966). Accordingly, in North America, populations of most species of ungulates have irrupted, when manipulated (predator removal) some have a history of recurrent irruptive fluctuations (see references cited by Keith, 1974). Ungulate irruptions have been characterized by a varying period of largely exponential increase to levels exceeding food supplies, and a catastrophic decrease, to much lower densities (e.g. Keith, 1974).

The pomarine jaeger (Stercorarius pomarinus) is highly nomadic, moving to breed in areas where lemmings are abundant. It is strongly territorial (Lack, 1968a). Maher (1970) showed that territory size and breeding density in the pomarine jaeger varied in accordance with the cyclic density of lemmings. The short-eared owl (Asio flammeus) in England also takes up new territories each year (Lack, 1968a). Lockie (1955) reported that during a vole plague in Scotland, the number of breeding short-eared owls was high. Both owls and voles remained at high densities the foll-

owing spring. But by June, the voles had declined steeply in numbers, nearly all owls departed, deserting their nests, and only two pairs remained. Of these two pairs, only one raised some young. Hence, the breeding density of the short-eared owl fluctuated markedly with fluctuating prey densities. This in contrast to the permanently territorial, and obstinate, tawny owl and Ural owl in Southern's (1970) and Lundberg's (1979) studies.

Also the data by Keith et al. (1977) on the response in breeding density by great horned owl to the snowshoe hare's 10-year-cycle partly fit the general prediction; the breeding density of great horned owls increased three-fold during the increase phase of the hare cycle, during the hare decline the breeding density decreased. Although the great horned owl is permanently resident, it is expected to be a JS-strategist since its life span probably is shorter than the ten year prey cycle (cf. Adamcik et al., 1978). Therefore, during the hare increase phase, the owls should respond by a decrease in territory size through territorial budding. However, note that we do not know if the increase in breeding density of great horned owl really was a consequence of territorial budding in the sense outlined above.

As mentioned above, in spite of the variable production of acorns MacRoberts and MacRoberts (1976) found that in their study area the number and distribution of groups of acorn woodpeckers remained essentially the same throughout the study; but the number of individuals constituting the groups changed in most cases. In Table 1 I have recalculated the data in MacRoberts and MacRoberts (1976, pp. 55-56) on the reproductive success of the acorn woodpeckers. The average number of young fledged per adult ranged from 0.20 to 0.28 while the average number of young fledged per group ranged from 1.06 to 1.28; thus in this obstinate strategist, both the production of young and the number of social units were remarkably stable from year to year. In contrast, in Stacey's (1979) acorn woodpecker population with less stable social organization (see above), the average number of young fledged per adult ranged from 0.4 to 1.1 ($\bar{x} = 0.77$). Moreover, Brown (1974) reported that the non-social scrub jay (*Aphelocoma coerulescens*) has a higher reproductive rate than the group breeding Mexican jay (*Aphelocoma ultramarina*) and invasion years are regular phenomenon in the non-group breeding scrub jay, Steller's jay (*Cyanocitta stelleri*), blue jay (*Cyanocitta cristata*), and piñon jay (*Gymnorhinus cyanocephalus*), but they are unknown in the group

TABLE 1

Reproductive success of acorn woodpeckers according to MacRoberts and MacRoberts (1976, pp. 55-56).

	NUMBER OF GROUPS SAMPLED (total number of adults)	TOTAL NUMBER OF FLYING YOUNG	TOTAL NUMBER OF YOUNG FLYING PER ADULT	TOTAL NUMBER OF YOUNG FLYING PER GROUP
1972	7 (31)	8	0.26	1.14
1973	16 (83)	17	0.20	1.06
1974	18 (82)	23	0.28	1.28
$\bar{x} = 0.25$, S.D. = 0.04 $\bar{x} = 1.16$, S.D. = 0.11				

breeding Mexican jay. In accordance, Woolfenden (1975) emphasized the overall population stability of the group breeding Florida scrub jay (a subspecies of scrub jay) in his study area.

The overall critical test of these predictions would be to disrupt the social system in a population of group breeders, e.g. by a consistent removal of all alpha individuals (breeders) before each breeding season; thereby inducing frequent symmetrical territorial contests. If this experiment would result in a decreased average territory size, a decreased average brood size but an increased overall production of young, and, above all, a decreased population stability, then the general theory presented in this paper would be strongly corroborated.

VOLE POPULATION CYCLES

The theory presented here is applicable also to population cycles in small rodents, where the following issues are generally observed (cf. Krebs and Myers, 1974).

In interannually cyclic small rodent populations, no low phase individuals are alive in the subsequent peak or decline phases. The phase of increase in many voles is associated with an extended summer breeding and possibly winter breeding. In the peak phase the summer breeding season is shortened and winter breeding is absent. Age at sexual maturity is increased in peak populations. Adult mortality rates are low in the increase and peak phases, and are high in the decline phase and also in the phase of low numbers. Juvenile losses are high in the peak phase and in the decline phase. Usually, the decline phase coincides with the late winter and spring season, i.e. at a time of year when food is sparse.

The extended breeding season and occurrence of winter breeding at low and increasing rodent densities indicate that at these low densities food is not limiting reproductive success. In contrast, the shortened breeding season and absence of winter breeding at peak densities can indicate that at high rodent densities food is critical for reproductive success and population growth. Recently these views have been supported by feeding experiments on small rodents (Taitt, 1981; Taitt and Krebs, 1981). By supplying Peromyscus maniculatus and Microtus townsendii with extra food, these authors demonstrated that the rodents significantly (1) extended

their breeding season, (2) increased in density, and (3) decreased their home range size. Peromyscus also responded by (4) reaching sexual maturity at a lower weight and by producing more young; all in comparison with rodents in control grids where no extra food was offered. Accordingly, a rodent present in the low or increase phase will probably not be affected by a food shortage (cf. Fig. 2, case i, Type I). Thus, according to the theory presented here (prediction ii, p. 22), such an individual will allow some of its offspring to breed and utilize the super-abundant resources. This will bring about an accelerated population growth (cf. Fig. 2, case i, Type II). When the rodent density increases, it will be more likely that the current individuals will be affected by a food shortage. This may explain why age at sexual maturity increases progressively in late increase phase and peak phase; i.e. because they are close to food ceiling more and more individuals prevent their offspring from breeding. At high densities, the overall reproductive success is probably more sensitive to a reduced food production (e.g. during the winter season) than at low densities (cf. Fig. 2, case ii). This can explain the high juvenile losses in the peak phase. In addition, a decrease in food availability can at high densities bring about high adult mortality rates (cf. Fig. 2, case iii, Type II). Food shortage may also force the individuals to struggle for territorial enlargement. These factors together are indeed sufficient for a population decline. Yet, they do not explain the often drastic decrease phase and long-lasting low phase. However, Pearson (e.g. 1971) and Keith et al. (1977) have demonstrated that predators by a delayed numerical response are able to deepen the decrease phase of voles and snowshoe hares, respectively, and to delay a recovery.

Interestingly, many island populations of small rodents, with a small number and variety of predators (e.g. Krebs, 1979; and references cited by Gliwicz, 1980, p. 115), usually attain higher mean densities than mainland populations of the same or comparable species (see review by Gliwicz, 1980). In addition, in contrast to cyclic mainland populations, many island populations have a great stability in numbers, often fluctuating only on an intraannual basis (Gliwicz, 1980). Since the population density on these islands remains at a high level in all generations it is likely that the majority of the rodents will be affected by seasonal changes in food availability (cf. prediction i, p. 22). Therefore, the majority of individuals will probably be obstinate strategists,

especially the spring generations (These are early cohorts which consist of individuals born early in the season. These individuals reach sexual maturity during their first season, in contrast to the late cohorts which do not reach sexual maturity until next season.) which together with the late cohorts constitute the overwintering individuals (Gliwicz, 1980); surviving the annual resource low. Accordingly, in island populations the early cohorts have the largest home ranges and the highest degree of utilization of the best microhabitats, whereas the late cohorts show the lowest values of these indices (Gliwicz, 1980). Thus, the individuals holding a high potential in the social hierarchy, i.e. mature females, come from early cohorts and are not found at all in the late cohorts (Gliwicz, 1980). In fenced populations of Microtus arvalis, Chełkowska (1978) observed that at high densities, social aggregations consisting of young siblings were formed; often occupying a common range.

Reproduction in island rodent populations is lower than in mainland populations. According to references cited by Gliwicz (1980) this is mainly due to a shorter breeding season, later maturation of females, and a limited number of females participating in reproduction; the two latter observations are typical of obstinate strategists while the former indicates that the rodents are close to food ceiling. Gliwicz (1980, pp. 129-130) cites several experiments in which the food supply of island voles was increased artificially. The voles reacted to this with a change in several aspects. The home range size, earlier strongly differentiated between successive cohorts, became much more uniform. This was due to a considerable decrease in the home range size of individuals from early cohorts which previously held the largest home ranges. Simultaneously the number of mature females increased, probably because with decreased home range size more female could attain suitable home ranges (Gliwicz, 1980). Importantly, also winter reproduction took place and the winter survival increased slightly; further stressing the view that, normally, island populations of rodents consistently are close to food ceiling.

In essence, the annual demographic pattern of island populations of rodents resembles that of the peak phase of interannually cyclic mainland populations; i.e. an increase in summer, peak in autumn, and decline in winter. It might be that the low occurrence of predators, and thereby the absence of their delayed numerical response, is responsible for the fact that island populations do

not continue to decrease in the spring and remain low until next breeding season as do cyclic mainland populations (cf. Krebs, 1979).

CONCLUDING REMARKS

Concludingly, I have demonstrated that it is not generally true that territory size changes according to changes in food supply. Some animals are capable of maintaining a fixed territory size even if the food varies from year to year. By necessity, this increases population stability. This is not because any self-regulating process at the population level has evolved, but because every individual's selfish strive to maximize its inclusive fitness makes it possible for a few individuals to, by kin selection, monopolize the breeding position in each territory. In contrast, some animals have nothing to gain in fitness by monopolizing the breeding position within a territory or they are not capable of maintaining a fixed territory size; such population can not be stable.

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5 PREY CONSUMPTION OF A RED FOX POPULATION IN SOUTHERN SWEDEN

Torbjörn von Schantz*

INTRODUCTION

This study was carried out as a part of an integrated research project concerning relationships between vertebrate predators and their prey animals in an open field area in southernmost Sweden. The analysis of the fox diet was based on the analysis of 1,028 scats, and 162 prey remains found at fox dens. The percentage of weight of the prey items in the diet was calculated; *Lagomorphs* was the most important prey throughout the year. The number of foxes in the population and their monthly prey demands were estimated and analysis of the annual predation showed that 10 to 15 percent of the annual production of each of the dominant prey populations was consumed by the foxes.

The diet of the red fox has been studied during the last five decades (for review of literature see; Jensen and Sequeira, 1978, Lutz, 1978, and Korschgen, 1959). Most studies have described the qualitative composition of the diet. Only in a few cases have a quantitative analysis been made and there have been few attempts to estimate the impact of fox predation on the prey populations (Pils and Martin, 1978, Goszczyński 1977, Goszczyński et al., 1976, Ryszkowski et al., 1971, and Korschgen, 1959).

This study evaluates the fox diet composition, and the impact of fox predation on the prey populations, calculated from data on the number of foxes in the population and their food demands.

THE STUDY AREA

The Wildlife Research Group at the University of Lund examines a community of vertebrate predators and their prey animals in the Revinge area, southernmost Sweden (55.42°N, 13.25°E). The project aims to examine factors regulating numbers of predators in the community and also to examine the impact of predators on the prey populations.

The study presented in this paper was carried out between August 1974 and March 1977 in the Revinge area. The study area, about 45 km², was earlier agricultural, but since 1965 it has been used for military training. The area contains open fields grazed by cattle interspersed by coniferous plantations and copses of deciduous trees. Dry parts of the area are densely inhabited by rabbits (*Oryctolagus cuniculus*). The area also contains extensive marshes populated by voles, primarily *Microtus agrestis* and *Arvicola terrestris*.

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Fig. 1. Study area and distribution of main habitats.

Methods

The food habits of adult foxes were determined by analysis of scats, collected twice each month on a special scat-collecting-route, approximately 7 km long, covering all types of habitats. The scat analysis was performed as described by Lockie (1959) and Goszczyński (1974). Determination of mammalian hair was made according to Brunner and Coman (1974). When calculating the percentage of weight in the diet for the prey items I used the correction factors of Lockie (1959).

The diet of cubs during the denning period was determined by registration of prey remains at the dens. Mean weight of found prey species was estimated and multiplied by the number of occurrences to yield the percentage of weight for each prey type. The calculation of food demands of the foxes was based on the results of Sargeant (1978).

To determine the number of foxes in the population, I counted, using a searchlight, foxes at night in 140 plots, in all covering 300 hectares. This was done five times in late autumn and five times in late winter every year. Telemetry data (von Schantz unpubl.) showed how long the foxes spent in open habitats where they could be seen. The counting plots were distributed only in such habitats. That is, if the foxes for example spent 80 percent of their time in "visible" habitats during night, I consequently assumed that the population size calculated on the basis of the counts was 80 percent of the true population. Further details on this method and the assessment of its significance will be published elsewhere. The number of cubs was determined by counting the number of litters in the study area, and the number of cubs in a sample of litters during May and June.

RESULTS AND DISCUSSION

The diet

The percentage of total number of occurrences of fox prey items, based on scat analysis, is given in Table 1. There was no significant difference between

Table 1. Percentage of total number of occurrences of prey items in the fox diet, based on analysis of 1,028 scats. The figures are approximated to closest unit. *Lagomorphs* consist of rabbit (*Oryctolagus cuniculus*) and European hare (*Lepus europeus*), other small rodents consist of *Clethrionomys glareolus* and *Apodemus* sp. Thrushes and bigger birds have been considered as large birds. Only vegetables and fruit with nutritional value for the fox have been recorded. Carcasses, eggshells, garbage and occasional prey items, e.g. fish, cat, squirrel, etc. have been assign to miscellaneous.

Period	Lagomorphs	Arvicola terrestris	Microtus agrestis	Other small rodents	Large birds	Small birds	Insects	Veget- fruit	Miscel- laneous	Total number of occurrences	p (χ ²)
I Dec-Mar	46	2	26	3	5	6	3	1	6	435	p < 0.001 (38.0) I-II
II Apr-May	46	7	16	1	4	7	11	2	7	249	p < 0.01 (23.6) II-III
III Jun-Sep	40	7	10	1	6	7	18	7	6	856	p < 0.001 (92.5) III-IV
IV Oct-Nov	46	4	21	1	2	3	6	11	4	584	p < 0.001 (68.5) IV-I

the years, so I pooled the data from the same month each year. Consecutive months, with similar (no significant differences) diet, were put together in food seasons. *Lagomorphs* and, to a certain extent, small rodents dominated in all periods. Birds occurred less frequently in October and November, insects occurred most frequently in April to September, while vegetables and fruit were more common in the diet from June to November than in winter and spring.

Analysis based on frequency of occurrence does not give any accurate information on the relative importance of the different prey items. Large prey, such as *Lagomorphs* are underestimated, while small prey, such as *Microtus* will be overestimated. This is well illustrated by comparing Table 1 with Table 2, where I have used Lockie's correction factors and calculated the percentage of weight for the prey items. Insects and vegetables are excluded as their weight was negligible. This type of data illustrates better the relative importance of the different prey categories. It is also the only data that can be used, when working with scat analysis, to calculate the amount of consumed prey biomass or number of prey animals taken, during a specified period of time.

Lagomorphs were far the most important prey throughout the year. The smallest percentage (77) of *Lagomorphs* was in April (Fig. 2). In late May and in the beginning of June the rabbit kittens began to leave the burrows. The amount of *Lagomorphs* in the diet increased during this period to the peak value in July (91%). From April to October *Arvicola* was the second most important prey. *Arvicola* is less available for foxes during winter than *Microtus*, as *Arvicola* during this season seldom leaves its tunnels in the frozen ground (Jeppsson pers. comm.). *Microtus* make its tunnels in the litter (Hansson pers. comm.) and consequently is within reach of foxes also in winter.

Cub diet in may and June, based on prey remains found at dens, was dominated by *Lagomorphs* and large birds (Table 3). No remains of voles were found, probably because they are eaten whole. The percentage of occurrences of other prey items corresponds well to Englund's (1969) data from southern Sweden, based on stomach analysis. Therefore, I used his figures regarding the percentage of occurrences of voles in Table 3. Among small rodents, *Arvicola* was the main prey in the diet of adult foxes in May and June (Fig. 2). I therefore conclude that voles in the cub diet consisted of *Arvicola* only.

Table 2. Percentage of weight of prey items (corrected according to Lockie, 1959) in the fox diet, based on analysis of 1,028 scats. The figures are approximated to closest unit.

Period	Lagomorphs	Arvicola terrestris	Microtus agrestis	Other small rodents	Large birds	Small birds	Number of scats
Dec-Mar	86	2	9	1	2	1	230
Apr-May	78	11	7	<1	3	1	124
Jun-Sep	89	6	2	<1	2	1	374
Oct-Nov	87	5	6	<1	1	<1	300

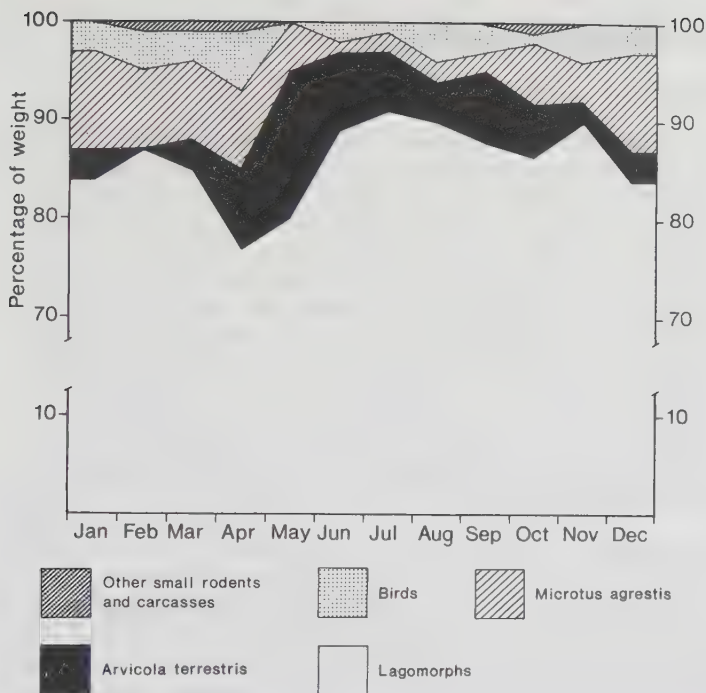


Fig. 2. Percentages of weight, on monthly basis, of prey items in diet of adult foxes, and of cubs from July and onwards (see p. 14). $N = 1,028$ scats.

The diet of adults and cubs in May and June, excluding small rodents, insects and vegetables, showed a significant difference ($p < 0.001$, $X^2 = 24.6$). The most important difference was the great amount of large birds in the cub diet. A possible overrepresentation of birds in remains outside dens, compared with mammals, is suggested by Pils and Martin (1978). They found, when digging out fox dens, that 50 percent of all "large bird" remains found were found outside the dens, while only 34 percent of all mammal remains

Table 3. Diet of the fox cubs during May and June, based on 162 prey remains collected at dens. The figures are approximated to closest unit.

Prey item	Percentage of total occurrences	Percentage of weight
Lagomorphs	40	52
Large birds	28	33
Small birds	4	<1
Voles*	15	2
Miscellaneous	13	13

* For voles, see the text.

October to February. It was further assumed that there was no adult mortality from February to September.

Food demands

Sargeant (1978) made a study on prey demands of adult and juvenile red foxes during the spring and summer cub-rearing period. Based on his paper, I calculated the prey demands for the foxes in the Revinge population. As the latter are approximately 60 percent heavier than those studied by Sargeant, their prey demands are accordingly higher. Therefore, estimated prey demands were 0.52 kg per fox and day for adult foxes and for subadults (25 weeks and older). I assumed that this figure was valid throughout the year. One week before whelping the vixens needed 0.69 kg per fox and day. During their first four weeks, the cubs had a weekly demand of 0.93 kg per cub, attributed to the vixen for providing milk to the cubs. At the age of 5–8 weeks, when the cubs are weaned, they needed 2.25 kg per cub and week, during the weeks 9–12 they needed 3.10 kg per cub and week, and during the weeks 13–24 they needed 4.14 kg per cub and week. The figures above include nonconsumed prey parts.

Impact of predation

When calculating the number of animals taken of the different prey species it is important to know whether the foxes preferred a certain size category of the animals in any of the prey populations, or if the various size categories were equally exploited. A good approximation for calculating the number of animals taken could be achieved by using mean weights of the disappearing fraction of the prey populations. However, this has been possible only for the hare (*Lepus europeus*), and the calculated number of hares taken, presented in Table 5, is based on such data (Frylestam unpubl.). Consequently, the calculated number of individuals taken of the other prey species, presented in Tables 5–8, are based on the mean weights of individuals in the prey populations, as computed from trappings.

The separation of rabbits and hares in Table 5 is based on a sample of 250 identifications of *Lagomorph* hair according to Brunner and Coman (1974). The largest number of hares in the diet occurred from February throughout May ($p < 0.05$, $X^2 = 4.3$, D.F. = 1). The earliest hare litters were born in February and the latest in October (Frylestam unpubl.). Such early and late litters probably were especially exposed to predation (Frylestam unpubl.), and this may explain the peaks in these months. The large number of hares in the fox diet from February throughout May may be explained by the foxes' thorough scanning of the ground when hunting for small rodents, which they did to a high extent during this period (Fig. 2). This probably caused many hare litters to become predated. In June and July there is a great production of rabbit kittens. During this period the foxes change to rabbit hunting which is reflected in the diet as a decrease in the amount of small rodents (Fig. 2) and a decrease in the amount of hares (Table 5).

Table 5. Consumed biomass, and calculated number of rabbits and hares eaten by the fox population in 1976. The figures on numbers of rabbits and hares eaten are approximated to closest ten. Mean weight of rabbits and hares were supplied by Jansson (unpubl.) and Frylestam (unpubl.).

Month	Proportion of Lagomorphs in the diet (%)	Consumed biomass Lagomorphs (kg)	Lagomorph species (%)	Consumed bio- mass rabbit (kg)	Rabbit mean weight (kg)	Number of rabbits consumed	Consumed bio- mass hare (kg)	Hare mean weight (kg)	Number of hares consumed
Jan	84	706	100	—	706	1.89	370	—	—
Feb	87	444	73	27	324	1.86	170	—	—
Mar	85	502	91	9	457	1.69	270	218	110
Apr	77	640	92	8	589	1.70	350	—	—
May	80	52 (juv)	448	478 (juv)	89	11	824	1.75	470
Jun	89	52 (juv)	490	530 (juv)	95	5	969	0.74	1310
Jul	91	1565	95	5	1487	0.67	2220	231	100
Aug	90	1719	100	—	1719	0.95	1810	—	—
Sep	88	1276	100	—	1276	1.53	840	132	50
Oct	86	1204	89	11	1072	1.69	670	—	—
Nov	90	1126	100	—	1126	1.61	700	—	—
Dec	84	949	100	—	949	1.63	580	—	—
		Σ 12076			Σ 11487	Σ 9760	Σ 579	Σ 280	

Tables 6 and 7 show the numbers of *Microtus* and *Arvicola* taken, respectively. The annual amount of consumed biomass were approximately the same for these two species.

Eighty occurrences of large birds could be determined to species, 20 of which were pheasants (*Phasianus colchicus*). In Table 8 it is assumed that 25 percent of all large birds were pheasants, in all periods. Seventy percent of the annual fox predation occurred during April to June, the denning period.

Rabbits constituted nearly 80 percent of annual food demands of the fox population (Fig. 3). *Arvicola*, *Microtus*, hares, and birds were all equally important as supplementary food and they contributed less than 20 percent to the foxes' annual prey consumption. If foxes, during the prey species'

Table 6. Consumed biomass, and calculated number of *Microtus agrestis* eaten by the fox population. Numbers of *Microtus* eaten are approximated to closest hundred. Mean weight of *Microtus* was assumed to be 30 g from March to September and 21 g from October to February (Hansson unpubl.).

Month	Percentage of weight in the diet	Consumed biomass <i>Microtus a</i> (kg)	Number consumed
Jan	10	84	4,000
Feb	8	41	2,000
Mar	8	47	1,600
Apr	8	66	2,200
May	5	28	900
Jun	1	6	200
Jul	2	34	1,100
Aug	2	38	1,300
Sep	2	29	1,000
Oct	6	84	4,000
Nov	4	50	2,400
Dec	10	113	5,400
		Σ 620	Σ 26,100

Table 7. Consumed biomass, and number of *Arvicola terrestris* eaten by the fox population. Numbers of *Arvicola* eaten are approximated to closest ten. Mean weight of *Arvicola* was assumed to be 115 g from March to September and 100 g from October to February (Jeppsson unpubl.).

Month	Percentage of weight in the diet	Consumed biomass <i>Arvicola</i> t, (kg)	Number consumed
Jan	3	25	250
Feb	0	0	0
Mar	3	18	160
Apr	8	66	570
May	15 2 (juv)	84 18	890
Jun	8 2 (juv)	44 20	560
Jul	6	103	900
Aug	4	76	660
Sep	7	102	890
Oct	5	70	700
Nov	2	25	250
Dec	3	34	340
		Σ 685	Σ 6,170

reproduction seasons, preyed to a very high extent on the juveniles, then the calculated number of prey animals taken during the summer could be greater than presented in Tables 5–8. It is obvious that these figures are rough, as young voles, that have not yet left their nests, are not within the calculation of the mean weights in the vole populations. Furthermore, naked juvenile voles will probably not leave any remains in fox scats. However, Englund (pers. comm.) found only few juvenile voles in the fox stomachs he analysed (Englund 1965). Another source of error is to what extent taken large prey are eaten. That is, do foxes leave a large prey once they have filled their stomach or is the prey cached, and later fully exploited? Data presented by Macdonald (1976) suggest that foxes do exploit all their food caches, and that is assumed in this paper.

The annual number of main prey species taken by the fox population, suggest that 10–15 percent of annual prey production was exploited (Table

Table 8. Estimated number of pheasants (*Phasianus colchicus*), approximated to closest ten, eaten by the fox population. The numbers are calculated from the assumption that 25 percent of all occurrences of large birds were pheasants, in all periods. Mean weight of pheasants was assumed to be 1.1 kg from October to June and 0.8 kg from July to September (Göransson unpubl.).

Period	Consumed biomass pheasant (kg)	Number consumed
Dec–Mar	17	20
Apr–Jun	174	160
Jul–Sep	21	30
Oct–Nov	20	20
	Σ 232	Σ 230

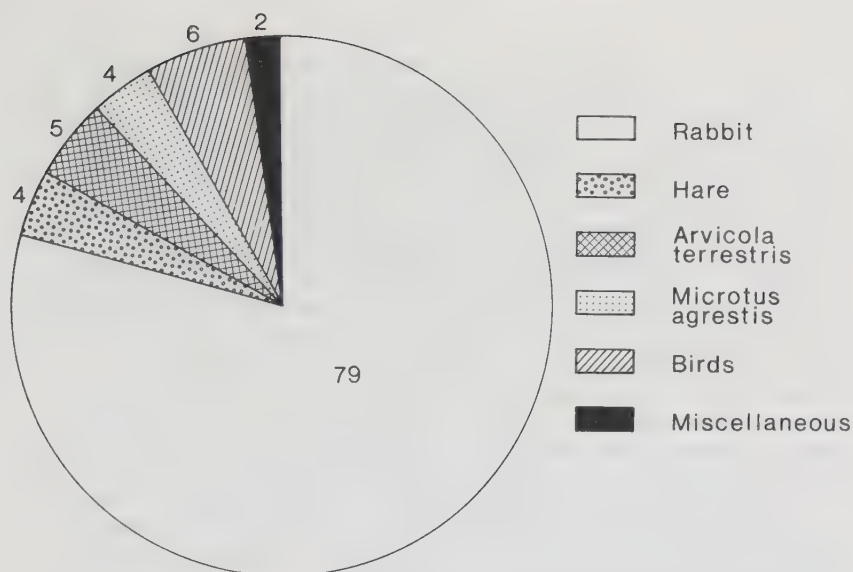


Fig. 3. Percentage of weight of prey items in total annual consumption of the fox population.

9). No data on annual production of *Arvicola* was available. Other small rodents, *Clethrionomys glareolus* and *Apodemus* sp., were exploited to a very small extent (Fig. 2), i.e. 1–2 percent of annual production. This agrees well with Macdonald (1977) who showed that foxes do not prefer these species in a comparison with *Microtus*. In spite of the dominance of rabbits in the foxes' diet they were affected to a smaller extent by the foxes than *Microtus*, which only contributed 4 percent to the foxes' annual prey consumption (Fig. 3).

Preliminary analysis of total predation of all the predators in the study area, suggest that foxes were responsible for 30 percent and 20 percent, respectively, of the total predation on rabbit and *Microtus*. Only 35 percent

Table 9. Percentages of annual prey production of newborn young, or hatched chickens, eaten by the fox population in 1976. Estimated prey production figures were kindly supplied by; Jansson (unpubl.) for rabbits, Frylestam (unpubl.) for hares, Hansson (unpubl.) for *Microtus*, and Göransson (unpubl.) for pheasants.

Prey species	Number consumed per year	Annual production	Percentage consumed of annual production
Rabbit	9,670	90,000	11
Hare	260	2,100	12
<i>Microtus agrestis</i>	26,100	171,000	15
Pheasant	230	2,400	10

of the annual rabbit production was preyed upon by the predator community, whereas almost the total annual production of *Microtus* was taken. During the winter 1976–1977, with very severe snow conditions, the rabbit population decreased sharply from 820 animals per km² in autumn to 120 animals per km² in spring (Jansson unpubl.). In 1978 they had still not recovered, which indicates that the predators were able to delay population increase at this low density. The consequence of the rabbit crash was a decrease in fox reproduction to half the number of cubs, compared with the year before. This indicates that fox reproduction was limited by food supply. However, the constant number of foxes in autumn 1975 and 1976, in spite of a 60 percent increase of the rabbit population (Jansson unpubl.), suggests that in 1976 the fox population was limited by other factors than food.

Jensen (1970) showed that the hunting bag of hare, partridge, and pheasant increased by 50 to 100 percent during a rabies campaign against foxes in Denmark. In the Revinge area, hunters each year shoot 5–7 percent of annual production of hares and pheasants, which is a smaller amount than the foxes eat (Table 9). Consequently, if the fox population would be kept on a lower level by increased hunting pressure it is likely that the hunting bag of field game would increase. But this in itself does not imply that fox predation is a limiting factor for these populations.

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SPACING OF THE RED FOX VULPES VULPES (L) IN

RELATION TO FOOD SUPPLY

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SUMMARY

(1) The territory size of foxes as determined by radio-tracking were compared between the Grimsö area (low diversity of food and cyclic small rodent populations) and the Revinge area (high diversity and high abundance of food and with non-cyclic small rodent populations).

(2) The territories were, on the average, larger in the Grimsö area than in the Revinge area.

(3) In the Revinge area, the territories of non-breeding foxes were smaller and of lower food quality than those of breeders.

(4) The mean territory size in the Grimsö area did not change between years of different food density.

(5) The spacing of foxes is discussed in relation to reproductive success and social organization. We suggest that (i) the territory size of foxes in stable environments is primarily adjusted to optimize reproductive success of a pair, secondarily to permit a family group of optimal size to become established, and that (ii) in cyclically fluctuating environments where the period of the cycle is shorter than the life span of a reproducing fox, territory size is adjusted to optimize reproductive success as soon as permitted by food density (first year of increase). During cyclic lows, reproduction is inhibited and territory size kept constant. With food density increasing over that needed for optimal reproductive success of a pair, territory size still remains the same and group size is optimized.

INTRODUCTION

The red fox (Vulpes vulpes L.) inhabits a great variety of habitats in different biotas, living in territorial groups of 2-5 individuals (Macdonald 1980, Niewold 1980). We use the term "territory" in its broadest sense, i.e. "... whenever individual animals or groups are spaced out more than would be expected from a random occupation of suitable habitats ..." (Davies 1978). Only one male fox is resident in each territory and only one or occasionally two vixens reproduce (Macdonald 1980, Niewold 1980). Territory size of foxes varies according to habitats (Table 1). Macdonald (1977, in press) considered the spatial distribution of food to be a determining factor for territory size. In this paper we discuss territory size in relation to food resources, social organization, and reproductive success. We compare the spacing pattern of foxes in two different food environments, the Grimsö area with a low diversity of food and cyclic small rodent populations, and the Revinge area with a high diversity and abundance of food and with non-cyclic small rodent populations. We propose an alternative model for the relationships between food supply, territory size and social organization in the red fox, stressing the density of food as a key factor.

TABLE 1

Reported mean territory sizes of the red fox. Territory size is calculated as convex polygons (minimum area, minimum perimeter polygons) if nothing else is noted.

TERRITORY SIZE (km ²)			LOCATION	MAIN HABITAT	REFERENCE
Mean	SD	Range			
11.5 ^a					
			England, Cumbrian fells	open hill country	Macdonald in press
9.3			The Netherlands, Dwingeloo	heath and forest	Niewold 1980
9.3			USA, Wisconsin	farmland of low diversity	Ables 1969
8.4	4.6	4.3-18.7	Canada, Ontario		Voigt & Tinline 1980
7.5 ^b			USA, Minnesota	mixed land?	Storm et al. 1976
6.3	1.2	5.3-7.7	USA, Minnesota	mixed land	Sargeant 1972
5.6	0.4	5.1-5.8	USA, Wisconsin	farmland	Pils & Martin 1978
5.2	0.7	4.6-6.0	France, Chizé forest	deciduous forest	Maurel 1980
3.9	0.4	3.6-4.2	USA, Illinois	farmland	Storm 1965
2.5			The Netherlands, Deelen		Niewold 1980
2.3	0.1		England, Oxford	farmland	Macdonald in press
1.3	0.7	0.4-2.2	USA, Wisconsin	arboretum	Ables 1969
1.2			The Netherlands, Nat.Park Veluwezoom		Niewold 1980
0.9 ^a	0.5		England, Oxford	urban area	Macdonald in press
0.7			England, Oxford	suburban area	Macdonald in press
0.6			The Netherlands, Valkenberg		Niewold 1980
0.5	0.1	0.3-0.8	England, Bristol	urban area	Harris 1980

^a Calculated from best estimate of configuration

^b Recalculated as an elliptic area from length times breadth.

STUDY AREAS

The Grimsö Wildlife Research Area (140 km²) is situated in south-central Sweden (59° 40' N, 15° 25' E, Fig. 1), within the southern part of the boreal forest, the south taiga (Lindquist 1966). The Revinge area (45 km²) is situated 450 km to the south of Grimsö in the beech-forest region (Lindquist 1966) of southernmost Sweden (55° 42' N, 13° 25' E, Fig. 1). Fox shooting was prohibited in the major parts of both areas throughout the study. Prey densities and habitat distribution in the two areas are shown in Table 2 and Fig. 2. We have assumed that the high energy demands of reproducing foxes (Sargeant 1978) relative to the low prey densities during early spring make this period energetically critical to foxes. Hence, all figures below refer to the situation in spring.

Voles, mainly field vole (Microtus agrestis L.), predominated in the diet of foxes in the Grimsö area. Secondary foods were mountain hares (Lepus timidus), roe deer (Capreolus capreolus L.), birds, reptiles, and carrion (Lindström unpubl.). In the Revinge area rabbits (Oryctolagus cuniculus L.) predominated in the fox diet before the rabbit decrease in 1976-77 with field vole and water vole (Arvicola terrestris L.) as supplementary food (von Schantz 1980). After the rabbit decrease, field vole and water vole together were equally important as rabbits in the foxes' diet (von Schantz unpubl.). The only major prey common to both the Grimsö and the Revinge areas was the field vole. There was little difference in maximum spring density of field voles in the two areas. However, the mean density for a four years period, was higher in the Revinge area as the vole population of that area varied little between years while that of the Grimsö area fluctuated according to a four-year cycle (Hansson 1980a, Hörnfeldt pers. comm.). (During this study, 1977 and 1979 respectively, were peak and low years in the Grimsö area.) The occurrence of rabbits and the more frequent occurrence of water voles in the Revinge area made the abundance of favourite prey higher in that area than at Grimsö. The good feeding habitats of the Revinge area (rabbit and vole habitats) covered 40 % of the land while those of the Grimsö area (field vole habitats) covered only 15 %.

We measured the spatial distribution of the habitats on maps counting the number of habitat boundaries crossed by a system of 10 parallel transects. This measure is direct proportional to the total length of the boundaries of the covered area (Matern



Fig. 1. Positions of the study areas in Sweden.

1959, 1961). The transects were spaced 500 m apart and each was of five km according to the scales of the maps. Eight measurements in different directions were made (Table 3). According to this measure the landscape of the Grimsö area was more heterogeneous. Whereas the good feeding habitats (above) were smaller and/or of less regular shape and also less evenly spaced at Grimsö than in the Rëvinge area.

The severe winter of 1976-77 influenced food supply in both areas. In the Grimsö area weakened and dead roe deer became

TABLE 2

Habitats and prey biomass in the Grimsö and Revinge areas.

GRIMSÖ			REVINGE		
Main habitats	Coverage (%)	Dominating prey	Coverage (%)	Dominating prey	
Coniferous forest	60	bank vole (<i>Clethrionomys glareolus</i> Shreb.)	50	Open fields on mineral soil (rabbit)	
Bogs	20	-	20	Forest on mineral soil rabbit	
Clearcuttings and afforestations	15	field vole	20	Grazed and abandoned fields on peat soil field vole and water vole	
Arable land	3	-	7	Marsh and forest on peat soil -	
Prey	Average Biomass (kg/km ²)		Average Biomass (kg/km ²)		
	1977	1978	1979		
Main prey	10	2	1	rabbit ^b field vole ^c water vole	700-200 6 ?
Secondary prey	8	6	2		
bank vole ^d	4	7	5		
mountain hare ^e					

^a Biomass figures recalculated according to habitat distribution in the Grimsö area from figures on field vole density in various habitats given by Hansson (1978 and 1980b, similar area 80 km NE Grimsö).

^b Jansson unpubl. and von Schantz & Liberg in press.

^c Recalculated from Hansson pers. comm.

^d Grimsö inventorial programme, P.A. Lemnell & B. Hörnfeldt pers. comm.

^e Lindström, Angelstam, Lemnell, and Widén in prep.

TABLE 3

Analysis of habitat distribution in the Grimsö and Revinge areas. Mean number of habitat boundaries crossed per transect by a system of 10 parallel transects (5 x 5 km). Eight counts in different directions.

DIRECTION	ALL HABITATS				GOOD FEEDING HABITATS ^a ONLY			
	Grimsö x	SD	Revinge x	SD	Grimsö x	SD	Revinge x	SD
N	14.7	2.8	12.3	3.4	5.1	4.6	11.2	5.3
NNE	13.8	3.4	14.1	3.5	5.1	3.4	9.0	3.0
NE	17.3	3.0	14.3	3.3	4.8	2.7	8.7	3.0
ENE	16.5	4.5	13.0	2.6	5.0	4.0	8.6	2.8
E	17.4	4.5	11.2	3.8	5.2	1.8	8.3	2.4
ESE	16.5	1.8	10.2	3.5	5.2	3.3	7.1	1.7
SE	14.8	3.6	12.0	4.6	4.4	2.3	7.6	4.2
SSE	13.9	4.1	12.8	3.7	4.2	4.9	8.4	3.1
Mean per ten transects ^b	156±13 ^c		125±12 ^c		43.1±13 ^c		86.1±10 ^c	
Crossings per km ² good habitat ^d					11.5		8.6	
SD per mean ^e					0.70±0.21 ^c		0.37±0.08 ^c	

^a Grimsö: field vole habitat, Revinge: rabbit and vole habitats.

^b used as an index of landscape heterogeneity

^c 95 % c.l.

^d used as an index of habitat size and/or regularity (inverse relation)

^e used as index of spatial variability

temporarily available for foxes (1.5 roe deer died per km² during January to March 1977, G. Cederlund pers. comm.). In the Revinge area the rabbit population was reduced from 410 to 120 individuals per km² and the population had not yet recovered by 1979.

In two of the territories mapped during the low year of 1979 in the Grimsö area additional food was provided experimentally during winter and spring (Lindström unpubl.). The influence of this additional food on two other foxes tracked during the same period was supposed to have been small.

Figure 2A.



- | | | | |
|--|-------------------|---|---------------------------------|
|  | Lakes and rivers |  | Reforestation and afforestation |
|  | Bogs and farmland |  | Forest |

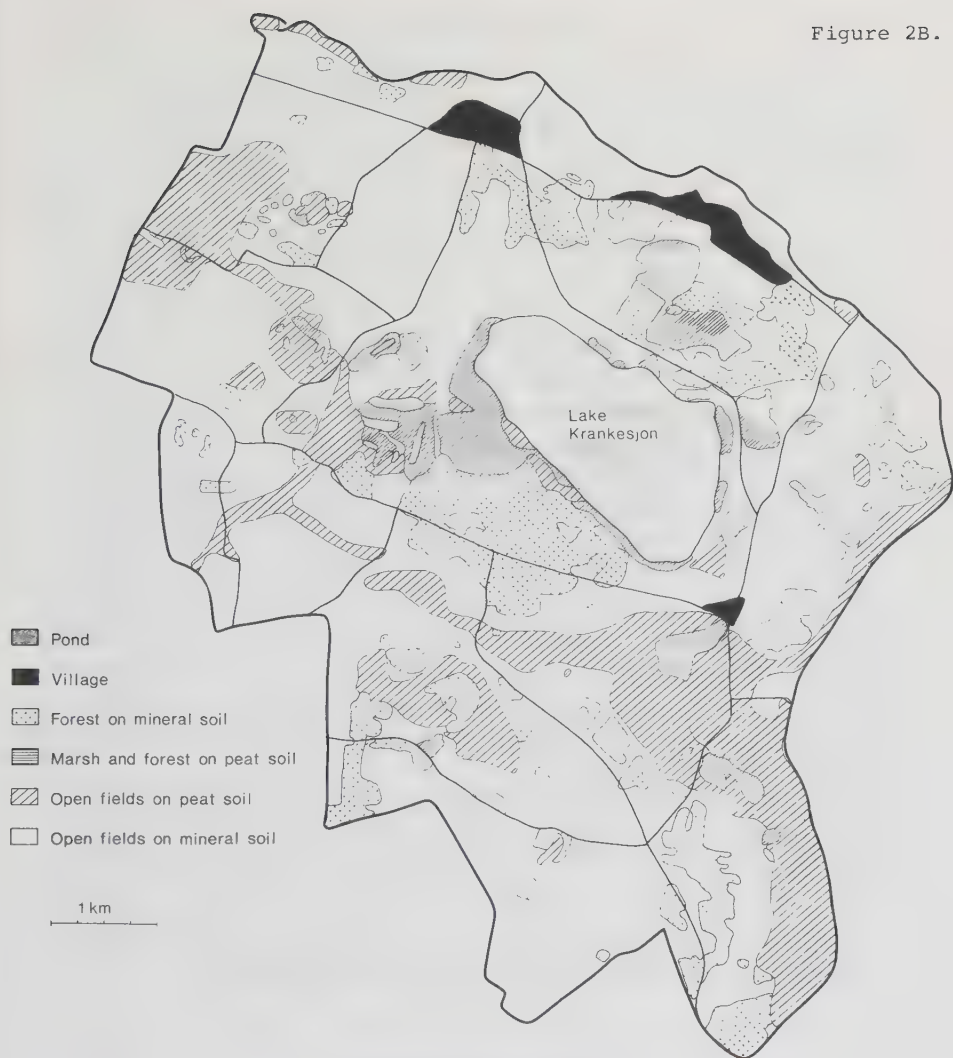


Fig. 2. Distribution of habitats within the study areas.

A. Grimsö.

B. Revinge.

FOX POPULATIONS

During years of high or increasing vole densities in the Grimsö area, the fox population increased due to high reproductive success and survival (Lindström unpubl.). Family groups were formed during these years as young females remained within their natal territories. This was evident from recovery rates of tagged juveniles and observations of both young and adult vixens simultaneously in two territories. This group formation also meant changes in reproductive success, breeding frequency, age structure, and sex ratio. During vole decline or low years the reproductive success of foxes was lowered and population size decreased. Thus, reproductive success was high in 1977 and low in 1978. In 1979 (year of low rodent density) litters were observed in the territories of foxes 11 and 25 (Grimsö, Table 4) where food had been provided experimentally. No litters were observed in the territories of foxes 15 and 19, which were situated seven and five km away from nearest bait station, respectively. The density of foxes varied between 0.2 (spring 1979) and 0.4 (spring 1978) individuals per km² (Lindström unpubl.). 37 % of all adult foxes experienced three or more potential breeding seasons (Lindström in press). The mean age of breeders only was still higher since the proportion of non-breeders was highest among the one-year old foxes (Lindström unpubl.).

The number of foxes during spring in the Revinge area was stable throughout the study (0.8 individuals per km²), whereas the number of litters and the autumn population was lower after the rabbit decrease than before (von Schantz & Liberg in press). The resident fox population in spring consisted of breeding individuals and non-breeding females (von Schantz 1981).

MATERIAL AND METHODS

Foxes were caught during 1976-79 in baited box-traps (Grimsö, Lindström 1979) and with leg snares (both areas, von Schantz in press) and equipped with radio collars. The foxes were classified according to age, sex, and reproductive status. Ten foxes at Grimsö and eleven at Revinge were radio-tracked during different seasons and in periods of different length (Table 4). Additional telemetry data, obtained from subadult and transient males, was discarded due to the migratory behaviour of these foxes.

TABLE 4

Radio-tracked foxes in the present study. The estimated territory sizes at Grimsö were calculated according to the asymptotic value of territory size as a function of the number of radio fixes. Breeding status: B; breeder, N; non-breeder. Territories at Grimsö where additional food was supplied are denoted with an asterisk.

AREA	FOX	No.	sex	age	breeding status	PERIOD OF RADIO-TRACKING	TRACKING TIME, OR NUMBER OF RADIO FIXES (p)	TERRITORY SIZE (km ²) observed	TERRITORY SIZE (km ²) estimated	FOOD DENSITY
Grimsö		01	female	ad	?	October 1976-January 1977	89 hours	8.1		high
Grimsö		03	female	ad	N	April 1977-July 1977	66 p	8.5	11.3	high
Grimsö		04	female	ad	B (?)	April 1977-May 1978 (total)	105 p	4.1	(3.3)	
Grimsö		05	female	ad	N	April 1977-July 1977	89 p	2.3	2.4	high
Grimsö		06	female	ad	B	January 1978-May 1978	26 p	3.5	4.2	low
Grimsö		07	female	ad	B	April 1977-July 1977	71 p	6.2	6.4	high
Grimsö			female	ad	B	May 1977-July 1977	39 p	6.7	9.9	high
Grimsö			female	ad	N	January 1978-May 1978	20 p	4.9	6.5	low
Grimsö		11	female	ad	N	February 1978-November 1979 (total)	106 p	5.3	5.3	
Grimsö		15	male	ad	B	February 1978-May 1978	16 p	2.0	3.0	low
Grimsö		19	male	ad	?	May 1979-June 1979	90 p	5.3*	5.6*	high*
Grimsö		25	female	sad	N	May 1979-September 1979	27 p	7.4	8.3	low
Revinge		09	female	ad	B	September 1979-October 1979	88 p	3.4	(3.2)	low
Revinge		12	male	ad	B	July 1976-August 1976	18 p	3.1*	4.5*	high*
Revinge		19	female	sad	N	March 1977-April 1977	49 hours	3.9		high
Revinge		22	female	ad	?	July 1977-August 1977	78 hours	3.3		high
Revinge		23	female	ad	N	November 1977	101 hours	3.4		moderate
Revinge		24	female	ad	N	January 1978-May 1978	96 hours	4.7		moderate
Revinge		25	male	ad	B	April 1978-June 1978	167 hours	2.1		moderate
Revinge		32	male	ad	B	April 1978-July 1978	86 hours	2.6		moderate
Revinge		33	female	ad	B	November 1978-February 1979	118 hours	6.0		moderate
Revinge		36	female	ad	N	May 1979-September 1979	243 hours	8.8		moderate
Revinge		39	female	sad	N	May 1979-September 1979	118 hours	4.6		moderate
Revinge			female	sad	N	October 1979-December 1979	51 hours	2.9		moderate
Revinge			female	sad	N	October 1979-December 1979	76 hours	2.5		moderate

Foxes at Grimsö were generally tracked intermittently from a mobile tracking unit (Cederlund & Lemnell 1979), obtaining one position per fox and sampling occasion. During most periods of tracking we sampled one position every 24 hours at varying times in the diurnal cycle. Fox No. 01 at Grimsö was tracked continuously for eight hours once a week from a fixed antenna system (Cederlund et al. 1979). The foxes at Revinge were tracked continuously for periods of 5-120 hours at irregular intervals.

ESTIMATION OF TERRITORY SIZE

Territory sizes were estimated as convex polygons. The few occasional long ranging trips outside the normally transversed area (cf. Niewold 1974) were excluded from the calculations by subjective judgement. The intermittent fixes probably gave a lower estimate of territory size than the continuous tracking. Thus, as an alternative to the convex polygon area of the territories mapped by the former method, we also calculated the asymptotic value of territory size as a function of number of fixes.

(A_{∞} in $A_N = A_{\infty} \times e^{\frac{\alpha}{N}}$, where A_N was the convex polygon area at the Nth fix and α was a constant for each fox.) This estimate also enabled a more strict comparison of territories determined from different number of fixes. When the observed value exceeded the extrapolated, the observed was used. The areas of lakes, completely surrounded by the territory, was subtracted when calculating territory size.

RESULTS

The mean territory size of foxes was 50 % larger in the Grimsö area than in the Revinge area (6.1 (observed value) vs 4.1 km², Table 5, Figs. 3 and 4). However, the small mean size at Revinge was due to the small territories of two breeding foxes before the rabbit decrease (mean 3.6 km², Table 6) and of five non-breeding females (mean 2.7 km², Table 7). After the rabbit decrease three breeding foxes occupied territories of 6.5 km² on the average (Table 6). The territories of foxes during years of low food abundance (and thus of low reproductive success) in the Grimsö area

TABLE 5

Mean territory sizes of foxes in the two study areas.

STUDY AREA	MEAN SIZE (km ²)	RANGE	SD	N	p ^a
Grimsö					
observed ^b	6.1	3.4-8-5	1.8	9	< 0.05
estimated	6.8	3.4-11.3	2.6	10	
Revinge	4.1	2.1-8.8	1.9	11	< 0.05

^aSmirnoff test of two samples of unequal size.^bFox No. 25 omitted due to small number of fixes.

TABLE 6

Mean territory size of breeding foxes in the Revinge area, before and after the decrease in rabbit density

RABBIT DENSITY	MEAN TERRITORY SIZE (km ²)	RANGE	SD	n(fox No.)	RABBITS PER TERRITORY
High	3.6	3.3-3.9		2(09,12)	820
Moderate	6.5	4.6-8.8	2.1	3(25,32,33)	590

TABLE 7

Mean territory size of breeding and non-breeding foxes in the Revinge area.
Data from fox No. 22 are omitted as her breeding status was unknown.

	MEAN SIZE (km ²)	RANGE	SD	n
Breeders	5.3	3.3-8.8	2.2	5
Non-breeders	2.7	2.1-3.4	0.5	5

and of non-breeding foxes in the Revinge area are more comparable, as the cost of reproduction does not have to be taken into account. Here, the difference was still larger, 4.8 (observed value) vs 2.7 km².

The indicated enlargement of the breeding territories at Revinge after the rabbit decrease meant that the amount of prey in

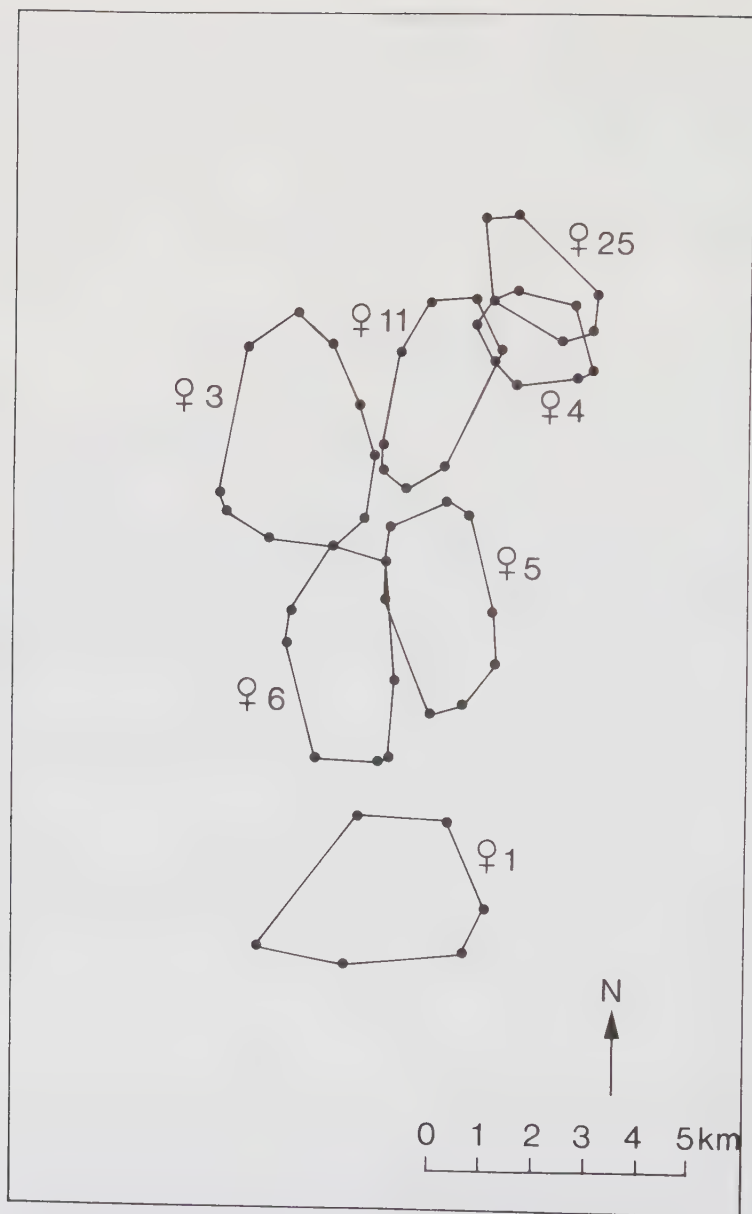


Fig. 3. Mapped territories at Grimsö.

A. During years of high vole abundance or when supplementary food was provided (fox No. 11 and 25).

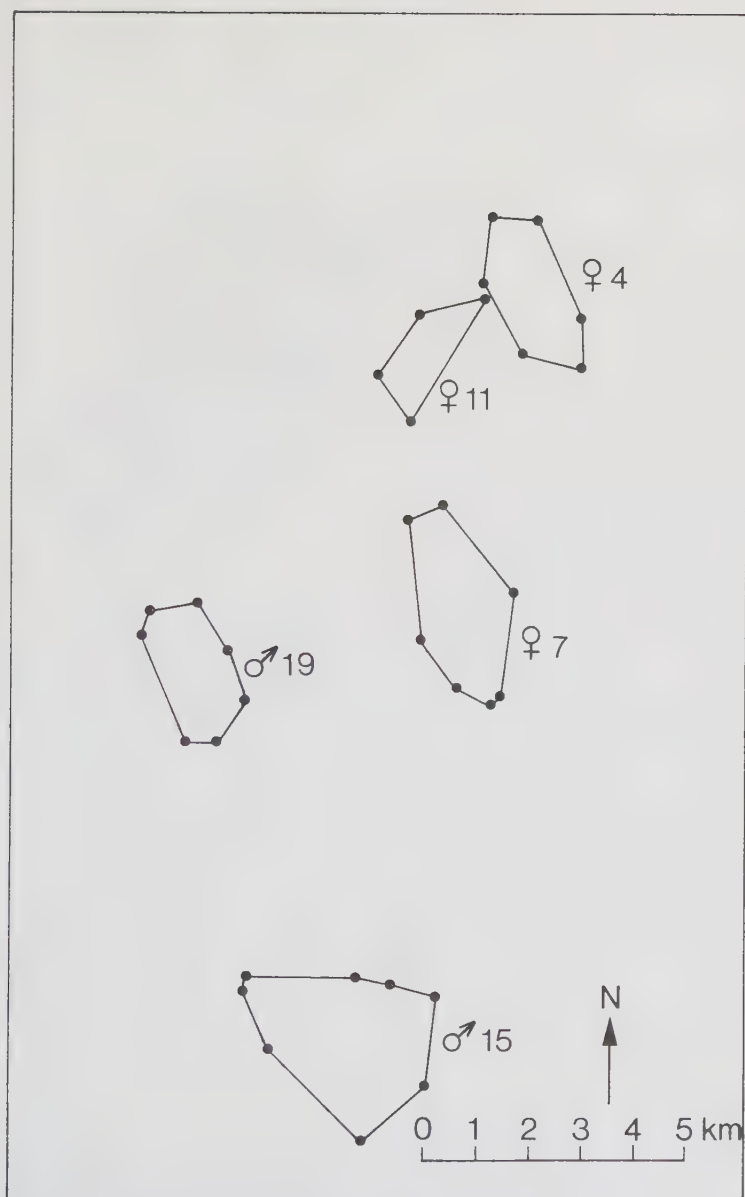


Fig. 3. Mapped territories at Grimsö.

B. During years of low vole abundance.



Fig. 4. Mapped territories at Revinge.

A. Breeding individuals and female No. 22 (whose breeding status was unknown).

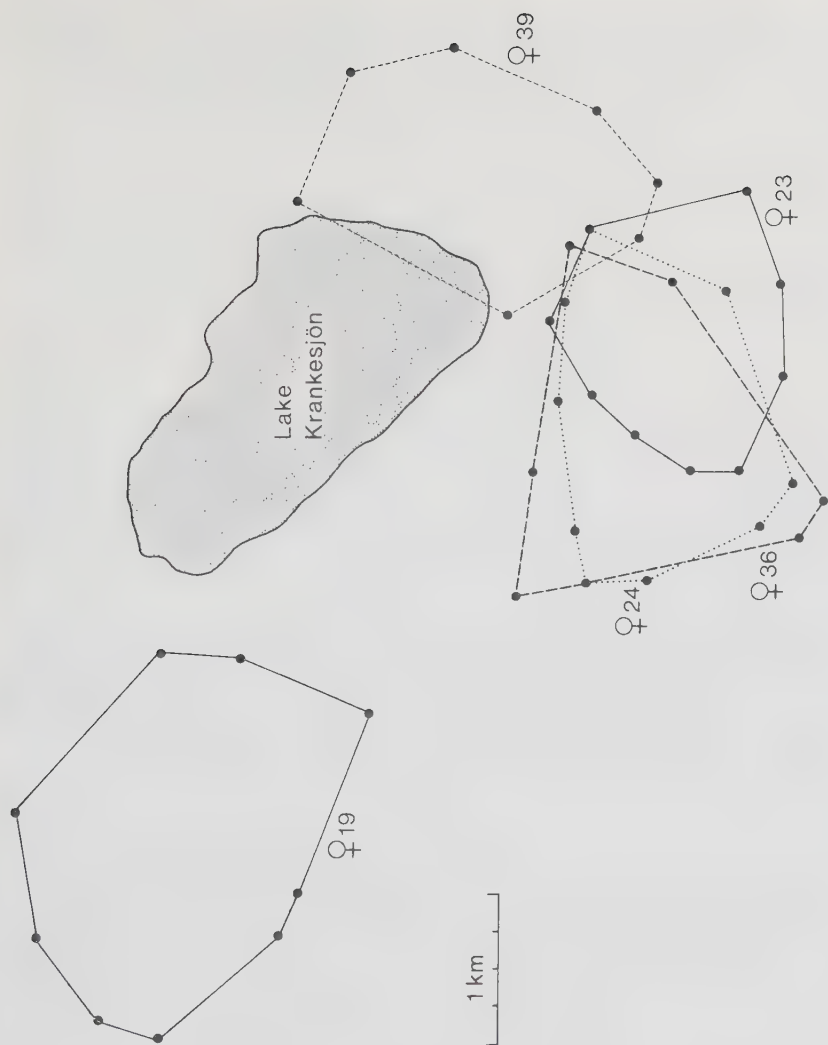


Fig. 4. Mapped territories at Revinge.

B. Non-breeding individuals.

each territory was partly maintained (approximately 600-800 rabbits per territory, Table 6). Furthermore, the territories of non-breeders at Revinge were considerably poorer than those of breeders; they were smaller and had lower rabbit densities (60 vs 150 rabbits per km², Table 8).

TABLE 8

Rabbit density in territories of breeding and non-breeding foxes in the Revinge area. Data from fox No. 22 are omitted as her breeding status was unknown.

	MEAN RABBIT DENSITY (ind. per km ²)	RANGE	SD	n	p ^a
Breeders	150	70-270	80	5	< 0.01
Non-breeders	60	40-80	10	5	

^a Mann-Whitney U test

In the Grimsö area the mean territory size showed no negative relation to food density when comparing different years (Table 9). Neither was there any indication of particularly small territories in females classified as probable subordinates (Table 4).

TABLE 9

Mean territory sizes (estimated values) in the Grimsö area in years of different food density. Territories mapped during 1979 in areas where additional food was supplied are included under "high" food density (see Table 4).

FOOD DENSITY	MEAN SIZE (km ²)	RANGE	SD	n
High	6.9	2.4-11.3	3.1	7
Low	5.1	3.0-8.3	2.3	5

Foxes numbered 03, 04, 05, and 06 at Grimsö (Fig. 3A) were tracked during spring and summer 1977. Three of them (03, 05, and 06) occupied territories adjacent to each other. Out of the 208 fixes obtained from these foxes, only two cases of trespassing territory boundaries were observed. The area between these and

the territory of fox No. 04 was in 1978-79 found to be inhabited by fox No. 11 (Fig. 3A and B). All these foxes were females. Furthermore, the configuration of the territories at Grimsö was much the same from year to year (Fig. 3A and B).

At Revinge small territories of non-breeding females were encompassed by breeding territories (Fig. 4A and B). The tendency for overlap between breeding foxes (especially males) was greater in the Revinge area than in the Grimsö area.

DISCUSSION

The same species may or may not be territorial depending on the distribution and abundance of its food (e.g. spotted hyena, Crocuta crocuta Erxl. (Kruuk 1972), Hawaiian honeycreeper, Vestiaria coccinea Forster (Carpenter & MacMillen 1976)). However, the common occurrence of territoriality among animals indicates the great advantages of monopolizing resources. Some animals have been shown to adjust territory size to food supply and thus attain territoriality in different habitats and in fluctuating environments (e.g. long-tailed jaeger, Stercorarius longicaudus Viellot (Maher 1970)).

The larger mean territory size at Grimsö as compared to Revinge (Table 5) may be interpreted as caused by the quantitative difference in food supply between the two areas (Table 2). The smallest territory mapped at Grimsö (No. 04, 1977, Table 4) was situated around the research station where waste products from slaughter etc. were present. The occurrence of scats with remains of carcasses and garbage was significantly higher among the scats collected inside this territory than outside (Lindström unpubl.). Furthermore, the suggested increase in territory size of breeding foxes after the decrease in rabbit density (Table 6) also indicated a quantitative relationship between territory size and food supply.

The energetic prerequisites for territoriality were studied by Carpenter and MacMillen (1976). For territoriality to occur, the basic cost of living (E) plus the added cost of being territorial (T) must be less than the sum of benefits from food resources obtained without territorial behaviour and added by being territorial (fractions a and b of the productivity (P) of the territory). By exchanging (P) by food density (D) times territory size (S)

and (T) by cost of territoriality per unit area (t) times territory size and by only considering cases when $E > aF$, their model can be rewritten:

$$E + tS \leq aDS + bDS \quad (1)$$

Thus, to attain territoriality in different habitats or to remain territorial in a fluctuating environment, the foxes may alter the size of the territory (S) or the basic cost of living (E).

There are two major ways in which E, the basic cost of living, may be altered in a fox group: (1) by changing the rate of reproduction (food demand of a reproducing pair with five young during lactation is 1.6 times that of a non-reproducing pair; Sargeant 1978), and (2) by changing group size. Hence, the difference in territory size and quality between breeding and non-breeding foxes at Revinge (Tables 7 and 8) may be interpreted in terms of the lower food demands of non-reproducing foxes (besides as a subordination effect, von Schantz 1981). The same may be valid for the lack of increase in territory size at Grimsö during years of low food densities (Table 9), since E was lowered by the lack of reproduction these years. However, the mean territory size at Grimsö never came close to the maximum measured for foxes (approx. 10 km^2 , Table 1). Then, why did not the foxes expand their territories and breed during vole lows? One explanation may be that the cost of increasing territory size would have offset the benefits during that year. Another explanation is afforded by MacArthur (1968). He showed theoretically that when an animal is exposed to a cyclically fluctuating prey it is advantageous if there are extreme shifts between breeding and unyielding survival; this would lead to more offspring than a moderate response would. By refraining from energetically detrimental fights for larger territories during vole crash or low years, the foxes at Grimsö were probably in better condition than otherwise for high reproductive success during the first year of increase in vole numbers. The territory size would thus be determined by the food supply during the increase year. As mentioned above ("FOX POPULATIONS") a large proportion of the breeding foxes experienced a complete vole cycle during their lives.

The number of breeding dens at Grimsö was constant for the years 1973-78 at one den per seven km^2 , except the low year of 1975 and the crash year of 1978 (Lindström 1980, unpubl.). Thus,

the mean territory size as estimated from radio-tracking ($6.1 - 6.8 \text{ km}^2$, Table 5) at Grimsö obviously contained resources enough to support a breeding pair and their young during the first year of vole increase. However, with a further increase in vole numbers, the territories did not decrease in size but remained the same throughout the vole cycle, both in size (Table 9) and in configuration (Fig. 3A and 3B). Instead, the numbers of foxes occupying the territories was indicated to increase, from one male and one female to one male and two females on the average (Lindström unpubl.). Following the vole crash, the fox family was reduced once again. Thus, we conclude that the basic cost of living (E) was modified both by variations in reproductive rate and in group size.

We never observed more than one litter per territory at Grimsö. In the Revinge area, observations before the rabbit decrease of mixed litters and of litters occupying closely situated dens (von Schantz unpubl.) indicated that more than one female bred per group. Neither mixed nor closely distanced litters were observed after the rabbit decrease. The density of rabbits immediately before the decrease was the highest measured at Revinge during this study (1974-79). The indicated occurrence of more than one female breeding per group might have been a first step in the formation of new independent groups. When food is abundant the dominant individuals have only few, if any, motives to prevent related subordinates from breeding. Also with an increase in food supply, a subordinate female, even if excluded from optimal food patches by the dominants (von Schantz 1981), may have access to suboptimal habitats that contain enough resources for reproduction. A new situation with smaller territories may develop as the breeding subordinate vixens and their female offspring become established as groups in territories of their own. Thus, a maximum sustainable group size probably exists. In areas of richer food supply than ours, the group size has been calculated to one male and three to four females (Macdonald 1977, Harris 1980). In the Revinge area, the average group size was three to four individuals (von Schantz unpubl.).

A HYPOTHETICAL MODEL OF SPACING IN THE RED FOX

Fig. 5 summarizes our proposal for the spacing of the red fox as a function of food density. Going from low to high food density

Figure 5.

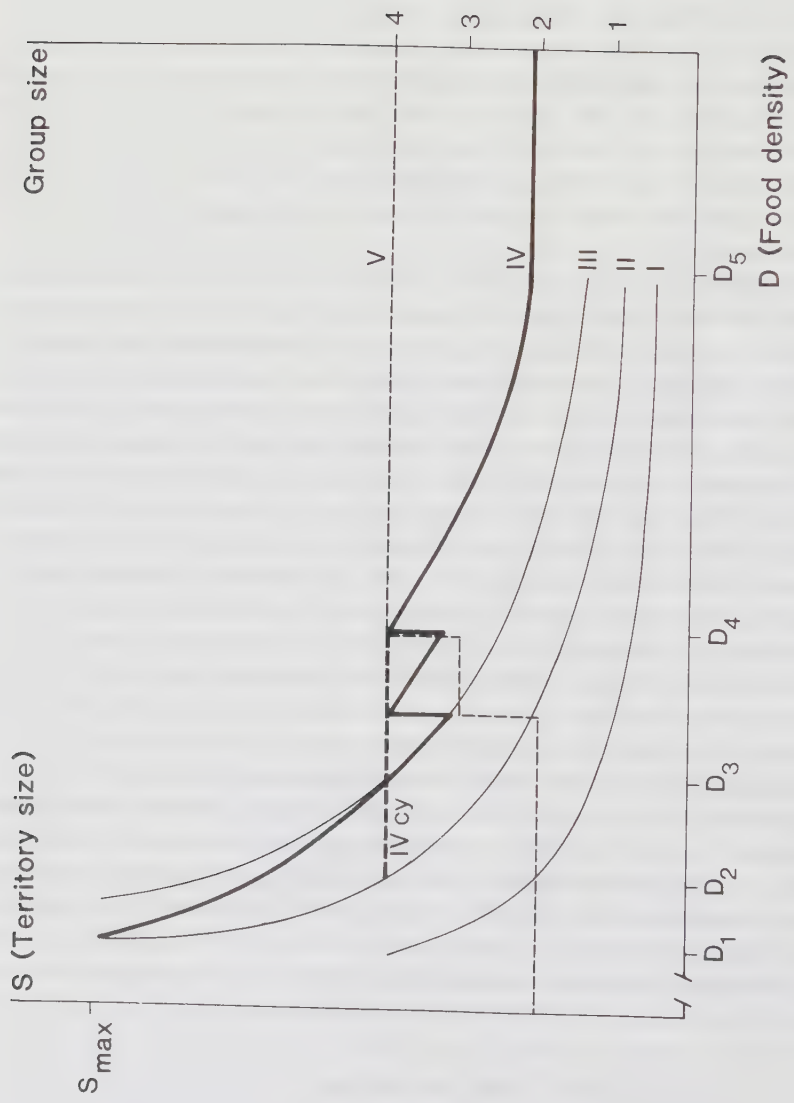


Fig. 5. A hypothetical model of red fox spacing as a function of food density.

- I Area demand of a single fox.
- II Area demand of a non-breeding pair ($2 \times I$).
- III Area demand of a breeding pair ($1.6 \times II$, Sargeant 1978).
- IV Territory size realized by the total group.
cy; in a cyclically fluctuating environment.
- V Group size.

Graph IV (realized group territory) should be interpreted in the following way:

- At D_1 Maximum sustainable territory size of a pair of foxes.
- (D_1, D_3) Stable environments: Territory size of a reproducing pair below optimal reproductive success.
- (D_2, D_3) cy Low in a cyclic environment: Minimum area needed for optimal breeding as soon as permitted by food density (first year of increase).
- At D_3 Territory size of a pair of foxes at minimum food density needed for optimal reproductive success.
- (D_3, D_4) Territory size approximately constant, group size increasing from two (D_3) to four (D_4).
- (D_4, D_5) Territory size decreases with increasing food density.
- At D_5 Something else, e.g. food distribution, dens etc., becomes limiting on territory size.

in this model, the following can be noted: (1) Below D_1 : The food density is too low to permit territoriality. (2) Between D_1 and D_3 : In a stable environment foxes live in territorial pairs which breed at an increasing rate of success the closer to D_3 they are. If this food density (D_1 to D_3) is experienced during a short-term low in a cyclic environment, foxes do not breed but remain as territorial pairs. Between D_2 and D_3 non-breeding foxes are able to keep a constant territory size in a cyclic environment (IVcy, Fig. 5). (3) At D_3 : Territory size and food density are in balance for the optimal reproductive success of a pair of foxes. (4) Between D_3 and D_4 : Territory size remains approximately constant but group size increases with increasing food density. (5) At D_4 : Group size has reached maximum (four in this case). (6) Between D_4 and D_5 : Territory size decreases with increasing food density. (7) At D_5 : The spatial distribution of food or some other resource (e.g. dens) becomes limiting on territory size.

In this model (Fig. 5), graph IV can be obtained from equilibria of costs and benefits of territoriality (eq. 1) at different

food densities and in a group of varying size. The costs should be linearly related to territory size and calculated for optimal survival and reproduction when possible (i.e. above D_3). It is assumed that maximum group size is four individuals. Thus, the foxes can not increase territory size at a certain food density above that depicted in graph IV without becoming super-territorial (a non-adaptive strategy; Colgan 1979, Getty 1979, Pleasants & Pleasants 1979). Furthermore, the benefits should increase with territory size up to a certain asymptotic level (above which the cost of defense is increased only), specific for each group size. Another vital assumption is that the inclusion of an additional subordinate group member does not increase the reproductive success of the group or the survival rate of the group members. The model refers to a system in balance. The momentary costs of increasing territory size from S' to S'' ($S' < S''$) are presumably much larger than the difference between maintaining territories of sizes S' and S'' , respectively. Thus, in a fluctuating environment the jumps in territory size at changes in group size would presumably be cancelled out by the advantages of traditional, well established boundaries. Accordingly, the territory size in a fluctuating environment would presumably adhere to the broken line between D_2 and D_4 (Fig. 5). The model is a deliberate simplification as it assumes uniformly distributed food. However, this may be an acceptable assumption for such a generalist feeder as the red fox, which is able to find something to eat in almost any habitat.

According to this model the fox population at Grimsö should have been oscillating from a point between D_2 and D_4 up to the point where group size equals three and back again during a vole cycle. The Revinge foxes should have been somewhere on the slope to the right of D_4 before the rabbit decrease and approximately at D_4 afterwards.

Macdonald (1977, in press) suggested that the territory size and configuration of foxes is determined primarily by the spatial distribution of the food needed for a pair to survive and breed; subsequently, the abundance of available food encompassed by this area determines the maximum group size which the territory could support. The same was suggested for the badger (Meles meles L.) (Kruuk 1978). We found the good feeding habitats to be smaller and less evenly distributed in the Grimsö area where the territories were larger than in the Revinge area. Thus, we can not

reject the hypothesis of Macdonald and Kruuk. Our model implies that the formation of family groups is not primarily dependent on the distribution of habitats as in Macdonald and Kruuk's model. A plausible force that may induce group formation is the increase in inclusive fitness (Hamilton 1964) gained by the dominant pair by allowing some of their offspring to remain within the territory. Thus, the survival and the chances of the offspring to inherit the territory would increase. However, this is a "luxury" which the dominant pair can afford only if the food density is sufficiently high. The advantages of living in family groups are further discussed by Macdonald (1980) and von Schantz (1981).

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Female cooperation, male competition, and dispersal in the red fox *Vulpes vulpes*

Torbjörn von Schantz

Schantz, T. von 1981. Female cooperation, male competition, and dispersal in the red fox *Vulpes vulpes*. – Oikos 37: 63–68.

Within the larger home ranges of breeding foxes (alpha-individuals), also non-breeding females (beta-females) with smaller home ranges, occur. Within each group, beta-females are presumably related to each other and to the alpha-individuals. Beta-females exploit suboptimal habitats, thereby avoiding competition with the alpha-individuals, which mainly utilize optimal habitats. After one breeding female died, a non-breeding female raised the deserted cubs. The non-breeding females regularly become pregnant, but abort or desert their young. By this type of female cooperation, offspring survival and inclusive fitness is maximized. In contrast, subadult males, that cannot contribute to inclusive fitness in this way, instead emigrate from their natal home range, competing for optimal habitats. One subadult female with a small number of suboptimal prey items within her home range, also emigrated.

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Внутри более обширных домовых участков размножавшихся лис (α-особи) встречаются также неразмножавшиеся самки (β-самки) с меньшими домами участками. Внутри каждой группы β-самки преимущественно общаются друг с другом и с α-особями. β-самки используют субоптимальные местообитания, избегая, таким образом, конкуренции с α-особями, которые в основном используют оптимальные местообитания. Если после размножения самка погибает, то неразмножавшаяся самка воспитывает оставленных детенышей. Неразмножавшиеся самки регулярно беременеют, но либо выбрасывают, либо оставляют разлзившихся детенышей. При таком характере кооперации самок выживаемость потомства и степень приспособленности в целом максимальны. В противоположность этому неполовозрелые самцы, которые не могут достичь такой степени приспособленности этим способом, эмигрируют из своихnatalных домовых участков и конкурируют за оптимальные местообитания. Неполовозрелые самки при низкой численности субоптимальных жертв внутри своих домовых участков также эмигрируют.

Introduction

The importance of inclusive fitness (Hamilton 1964) for explaining cooperative behaviour between animals living in groups is stressed in recent evolutionary theory (Brown 1975, Bertram 1976, Emlen 1978, Bygott et al. 1979). In the red fox *Vulpes vulpes*, a cooperative system has been described (Macdonald 1979) with several related females and one male in each group, in which only the highest ranked female bred. I report here on the resource partitioning between breeding and non-breeding individuals, and its effect on dispersal, in a red fox population in south Sweden.

Data on habitat utilization, home range, and dispersal were obtained from 2300 hours of radio-tracking of 15 foxes. The study area at Revinge, south Sweden, contains two main habitat types; dry grassland fields and pine plantations on mineral soil, inhabited by rabbits *Oryctolagus cuniculus*, and wet meadows on peat soil, populated by voles, primarily field vole *Microtus agrestis* and water vole *Arvicola terrestris*. These three species are main prey for the foxes in the area.

Social categories and resource utilization

The radio-tracked foxes were divided into the following social classes (One adult female (♀ 22) was radio-tracked only in autumn. Accordingly, I could not determine her social status. Therefore, data from this fox are only reported in Fig. 1): 1. *Alpha-individuals*; adult males with litters within their home range, and adult females that raised cubs, 2. *Beta-females*; adult females that did not raise cubs, and a subadult female (♀ 19) that settled in her natal home range and was shot there two years after she was radio-tracked, 3. *Emigrants*; including subadult males during early autumn (September), subadult males immediately before dispersal (October), and a subadult female (♀ 39) that dispersed during her first winter. Category 1 is called dominants and categories 2 and 3 are called subordinates.

The alpha-individuals spent more time in rabbit habitats than did subadult males tracked in September ($p < 0.001$), and beta-females ($p < 0.001$); the two latter categories spent more of their time in vole habitats (Tab. 1). In a social hierarchy it is reasonable to assume that the resources are exploited according to social rank of the individuals (for red fox see e.g. Vincent 1958). Observations on radio-tagged foxes (von Schantz unpubl.) indicate that a fox hunting for voles, during spring, has to hunt for seven hours per day to get enough food for its maintenance, whereas a fox hunting for rabbits has to hunt for five hours. In addition, a female with five weaned cubs has to catch three to four times as much food as a lonely fox. For a fox hunting for voles, this is probably an unachievable goal especially as she also has to make a greater number of provisioning trips compared with a fox that is able to catch rabbits.

Tab. 1. Habitat utilization of radio-tracked foxes of different social categories. In all pairwise comparisons differences between categories were significant ($p < 0.001$, chi-square-test, d.f. = 1), except when indicated by NS ($p > 0.05$). Data on alpha-individuals were collected during the whole year, whereas data on beta-females were collected during January to September. No major seasonal variation was recognizable.

Category	N (fox No.)	Mean percentage of observations in		Total number of observations in	
		Peat soil habitats (SD)	Mineral soil habitats (SD)	Peat soil habitats	Mineral soil habitats
α-individuals	5 (♂12, ♂25, ♂32, ♀9, ♀33)	37 (10)	63 (10)	403	709
β-females	4 (♀19, ♀23, ♀24, ♀36)	79 (15)	21 (15)	317	86
Subad ♂♂ (tracked in Sep)	2 (♂37, ♂38)	75 (7)	25 (7)	120	43
Subad ♂♂ (tracked in Oct)	3 (♂10, ♂30, ♂37)	34 (3)	66 (3)	59	121
Subad ♀39 (tracked in Oct–Nov)	1 (♀39)	36	64	36	63

Tab. 2. Home range size and resource availability. Figures on spring low densities (the spring of that year in which the fox was radio-tracked) of field voles (Hansson 1971) and rabbits (von Schantz and Liberg in press), based on the distribution of the different habitats in each home range, were used as an index on prey availability per home range.

Category	N (fox No.)	Home-range size in literature (SD)	Significance of difference*	Vole index (SD)	Significance of difference*	Rabbit index (SD)	Significance of difference*
Residents	5 (♂12, ♂25, ♂32, ♀9, ♀33)	530 (220)	p<0.05	970 (510)	NS	730 (200)	p<0.001
	4 (♀19, ♀23, ♀24, ♀36)			620 (110)	p<0.05	180 (60)	NS
						200 (70)	p<0.001
Emigrants	1 (♀39)	270 (50)	p<0.001		p<0.001		
	4 (♂10, ♂30, ♂37, ♂38)	130 (30)	p<0.001				

* t-test, two-tailed.

Rabbit-hunting was more profitable than vole-hunting also for domestic cats in the same study area (Liberg in press). I therefore regard habitats which are mainly used by the alpha-individuals, i.e. the rabbit habitats, as optimal. The low utilization of rabbit habitats by subadult males tracked in early autumn and by beta-females can be interpreted as a subordination effect (Brown 1975), i.e. a tendency for subordinates to avoid the dominants. In contrast, subadult males, immediately before dispersal, and the subadult female ♀39 (also emigrating), showed a similar habitat utilization as the alpha-individuals (Tab. 1); I return to this below.

Subordinate foxes also used relatively small home ranges, thereby further decreasing the probability of encountering dominants, at the cost of restricted access to prey (Tab. 2). Alpha-individuals had a higher number of rabbits within their home ranges than had beta-females and emigrants (Tab. 2). Home ranges of emigrants contained a similar number of rabbits but less voles ($p < 0.001$) than home ranges of beta-females. The small number of voles may be one reason for dispersal, as access to vole habitats were essential for resident subordinates (Tab. 1).

Female cooperation and reproductive strategy

The resident fox population consisted of breeding individuals, who lived in large home ranges, and subordinate females living in smaller home ranges within those of the alpha-individuals'. Previous studies (Jensen 1973, Storm et al. 1976) have shown that most subadult males leave their natal home ranges, whereas subadult females emigrate less frequently. In the present study I know the fate of 10 foxes marked as juveniles or subadults (eight males and two females). Of these all the males emigrated whereas one female emigrated and the other remained at home. From the low emigration rate of females from their natal home ranges it is reasonable to assume that the beta-females are related to alphas.

Almost all (10 out of 11) adult females, dominants as well as subordinates, shot in the study area were or had been pregnant. This is supported by beta-female ♀24, who was pregnant when trapped (early April) but did not raise cubs. The mechanism underlying the abortion or the desertion of the beta-females' cubs is unknown, but Macdonald's (1979) study on captive foxes indicates that it might be caused by social interactions with the alpha-female. Adult female ♀33 was not pregnant nor lactating when trapped in late April. However, in early May she adopted the litter of the alpha-female in her group who had recently died. After the adoption, ♀33 exploited rabbit habitats to a higher degree than before ($p < 0.05$), indicating that she had gained alpha-status. Access to rabbits is essential for raising cubs in the area (see above).

As radio-tracked beta-females visited the litters of the alpha-female in their overlapping home ranges only

occasionally, I conclude that they did not function as regular helpers (Skutch 1961, Macdonald 1979) but more as an "insurance back-up" (Emlen 1978) for the alpha-female, increasing the probability that the offspring would survive in the event of her death, as in the adoption described above. In addition, alpha-female tolerance of pregnant beta-females within her home range will lead to high inclusive fitness. The best thing for a beta-female, being related to the alpha-female, to do (if the alpha-female dies before giving birth), is to give birth herself. The second best thing for a beta-female (if the alpha-female dies after giving birth, and if the offspring of the beta-female is dead or aborted), is to adopt the alpha-female's offspring. The latter strategy evidently occurs and I can see no reason why the beta-female should not choose the best alternative if she gets the opportunity. Therefore, if the alpha-female dies before whelping, a beta-female (carrying a part of the alpha-female's genes) most probably takes her place and gives birth. Provided that the beta-females have access to enough resources for maintenance, the most important benefit for them to stay as subordinates probably is a relatively high chance of survival to the age and status necessary for getting access to the key areas, e.g. the rabbit habitats. An example of this is subadult female ♀ 19 (attributed to the beta-female category as she did not emigrate). She mainly exploited the suboptimal habitats (Tab. 1) and her home range had the same vole index as the other resident females' (Tab. 2). One subadult female ♀ 39 emigrated during the study. In spite of her home range being similar in size to the beta-females' home ranges (Tab. 2), she had access to a lower number of voles (Tab. 2) which probably forced her to exploit rabbit habitats (Tab. 1). This might have increased the frequency of encounters with the dominants, compelling her to emigrate.

Male competition and dispersal

As mentioned above, studies on red fox dispersal show that most subadult males leave their natal home ranges (Jensen 1973, Storm et al. 1976). If one looks upon the subadult males' "decision" to stay or emigrate as a result of the conflicting, or mutual, "interests" of the alphas and the subadult males, and compares this with the corresponding situation for the subadult females, it is logical that the subadult males emigrate. (1) Hamilton and May (1977) showed theoretically that parents who have dispersive offspring are selected for. They concluded, that any parent whose entire family remains to compete for space stands a finite chance of leaving no issue if any other member of the population have dispersive offspring, and it has no chance to have more than one offspring in the next generation. Thus, it lies in the alphas' interest to force some of its offspring to emigrate. It makes intuitive sense to assume that the alphas first expel those individuals that have the least to

contribute directly to the alphas' own inclusive fitness, i.e. the subadult males as they in contrast to their sisters neither can suckle the offspring if the alpha-female dies, nor can produce an extra litter. (2) Every group member is a potential competitor to the other group members. Thus, the smaller the future benefits a certain individual can expect from another group member, the less likely it is to accept the presence of the latter. Again, for the subadult males the cons exceed the pros (for the same reasons as under point (1)). (3) If both sexes stay, there is a risk of inbreeding, reducing the viability (Greenwood et al. 1978, Ralls et al. 1979) and the heterozygosity of the offspring which would be selected against (Lewontin 1974). If the young male succeeds his father, the remaining female group members are his relatives. To avoid inbreeding he must "arrange" that an unrelated female settles in the group and then mate with her. This action is contradictory to the

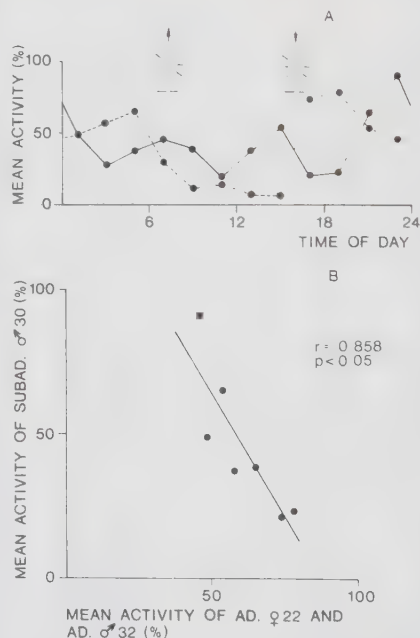


Fig. 1. A. Mean daily activity pattern, during late autumn, for subad ♂ 30 (solid line) and two adult foxes (ad ♀ 22 and ad ♂ 32) (broken line). B. Correlation of mean activity, during night (1700-0600) for subad ♂ 30 versus ad ♀ 22 and ad ♂ 32. Each point represents mean activity during a two-hours interval.

interests of all the female members of the group. Also a female that remains at home runs a risk of inbreeding. However, this is of less importance for her as she is related only to one group member of the opposite sex and thus only has to survive her father. In addition, if the young female wants to avoid inbreeding by mating with a neighbouring male, this is an action that is negative only to the interests of one of the group members, her father; he most probably can not prevent such cheating as it can be performed during a very short period and, perhaps, outside his own home range. Thus, a female that remains at home can more easily avoid inbreeding than can a male.

Although both sexes might gain in the same degree from lower mortality rate when remaining at home, males have a smaller motivation to remain at home than females. On the assumption that both female and male offspring are present, alphas benefit most, in terms of inclusive fitness, by letting female offspring remain at home and by compelling male offspring to emigrate. The very small home ranges of subadult males (Tab. 2) might be a result of such interference. Also, the home ranges of subadult males were situated on the outer edge of the alpha-individuals' home ranges. Another subordination effect is indicated by subadult male ♂ 30, which was tracked almost continuously during the last weeks before his emigration. This male hunted in the same habitats as alpha-individuals (Tab. 1), but differed in his daily activity pattern from adults tracked in the same period (Fig. 1). In contrast, subadult males tracked in September while still hunting in suboptimal habitats had a similar activity pattern as adults. Selection favours those females that can subsist on suboptimal resources as subadults (see above), whereas such a trait probably does not have the same adaptive value for males. As males seldom stay at home, there is only a weak, if any, selective pressure on them to behave cooperatively, e.g. by exploiting suboptimal habitats which is the cost for remaining at home. Thus for male foxes, as for most other living organisms, where a cooperative behaviour seldom is rewarded, selection favours those that have the best capability of competing for resources. Therefore, as competition with litter mates increases during autumn it could be favourable for subadult males to behave uncooperatively by exploiting optimal habitats (Tab. 1), as they probably are harassed by the family group anyhow.

Finally, red fox studies in North America indicate that female groups are unusual (see e.g. Sargeant 1972). Perhaps, the social system and resource partitioning described in this paper more easily evolves in patchy environments, as the one studied in Sweden. In patchy environments, individuals probably defend optimal habitats more easily than in homogeneous areas (Emlen and Oring 1977). In addition, a species that lives in habitats where only a few competing species exist has a wider food niche and more scope for diet division within species than species that live in an interspecifically com-

petitive environment (Roughgarden 1972). Thus, in ecosystems where this type of social organization have been described, besides the fox, only one equally large carnivore exists, namely the European badger *Meles meles*, whereas in North America several carnivores occur, of the same size as the red fox. Hence, the scope for diet division within a species may facilitate the resource partitioning between the different social categories described here and thereby also facilitate the evolution of red fox social organization.

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RED FOX NUMBERS, REPRODUCTION, AND SOCIAL ORGANIZATION AT

DIFFERENT PREY DENSITIES

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ABSTRACT

During a seven year study in southern Sweden the spring density of red fox (*Vulpes vulpes*) remained fairly stable, although its main prey, rabbits, changed markedly in density between years. The foxes responded to an increase in rabbit density with an increase in their rabbit consumption, and when rabbits were most abundant, probably more than one female in each fox group bred. Competition between breeding females within the groups lowered the foxes' reproductive success when the rabbit density began to decrease. During the rabbit decline, the foxes decreased their rabbit consumption and increased their consumption of voles, a resource that had been only weakly exploited before. From the second year of rabbit decline, only one female per group bred, and approximately half of the group members (and the population) were non-breeders, presumably mainly females. The rabbit density was exceptionally low in the last two years of the study (1980 and 1981). In 1980, when non-breeders still were present, the foxes' reproductive success was low. Although the rabbit density in spring 1981 equalled that in 1980 the number of foxes had dropped and few non-breeders were present. Yet, the production of fox cubs was considerably larger in 1981 than in 1980. I therefore question the helper-effect as an important selective force in the evolution of group living in the red fox, and suggest that group living in this species is induced by a temporary resource surplus within the territories.

INTRODUCTION

Among cooperatively nesting birds the presence of non-breeding adult helpers at the nest (Skutch 1961) seems to increase the production of fledglings compared with nests with few or no helpers (see reviews by Brown 1978, Emlen 1978). Typical of group breeders studied to date is a close genetic relatedness between the breeders and the non-breeding helpers in each group. Therefore, the importance of kin selection has been stressed in theories on the evolution of cooperative breeding.

Among the carnivores the presence of subordinate non-breeding adults within groups of genetically related individuals seems to be widespread (see review by Bertram 1978). In the cooperatively hunting blackbacked jackal (*Canis mesomelas*) the non-breeding helpers increased the production of young (Moehlman 1979).

The red fox (*Vulpes vulpes*) is a solitarily hunting canid that for long was believed to live in monogamous pairs. However, Macdonald (1979) found that foxes in England lived in family groups, normally including one male and several related females (of which the majority were barren), who used an area in common, a "group territory". Macdonald suggested that the non-breeding females, which were subordinate to the breeding females, might feed and guard the cubs of the breeding female within their group, thereby apparently contributing to the survival of the cubs. In the Re-

vinge area of southern Sweden the foxes live in groups similar to those in England (von Schantz 1981). In this paper I will examine the significance of "helpers" in the Revinge fox population.

THE STUDY AREA

The study area of about 45 km², at Revinge, south Sweden (55° 42' N, 13° 25' E), was previously cultivated, but has since 1965 been used for military training and cattle grazing. Dry sandy hills, partly planted with pine, occupy large areas. These are populated by rabbits (Oryctolagus cuniculus). Small woods and stands are scattered all over the area. About 20 % of the area is covered by marshy or wet meadows on peat soil, inhabited by voles, primarily field vole (Microtus agrestis) and water vole (Arvicola terrestris). Rabbit, field vole, and water vole were main prey for the foxes in the area (von Schantz 1980).

METHODS

Counting the adult fox population. Between autumn 1974 and spring 1981 the foxes were counted at night with the aid of a spotlight in 120 sample plots, totalling 280 hectares (eight per cent of all open habitats in the study area). The censuses were usually made on four or five occasions each in late autumn and early spring, respectively; in spring 1980 only two counts and in 1979 none at all were carried out. All the plots were in open habitats, where all present animals could be recorded. The proportion of foxes in covered habitats was estimated from telemetry data collected during the same seasons of the year. Based on the number of foxes counted in the plots, the population in the open habitat types was calculated. Obtained figures were extrapolated to total number of foxes in open habitats. Telemetry data were then used to add the number of foxes in covered habitats. For further details on this method see von Schantz and Liberg (in press).

Censuses of the rabbit population. Rabbits were censused simultaneously with the foxes in the sample plot counts. However, for rabbits there was no possibility of correcting for their spatial distribution with the aid of telemetry data as for foxes (von Schantz and Liberg in press). Therefore, the rabbit figures below are indices (minimum numbers).

Calculating of fox reproduction. In each spring from 1976 to 1981 the study area was searched for dens occupied by fox litters. Footprints of fox cubs, prey remnants and smell of fox scent and putrefying prey remnants at the den openings were signs of fox litters. Also, at weaning the cubs begin to play around the den and this wears off the vegetation around the den. These signs together made it easy to determine whether a den was occupied by a fox litter or not. To calculate litter size and total production of fox cubs I counted the number of cubs in as many litters as possible (some dens were situated in thick vegetation which made reliable counts impossible). Only litters in which the cubs were observed, and counted, at least twice have been considered in the analysis.

Fox diet. The foxes' food habits were examined by analysis of scats, collected in all habitat types throughout the year. The scat analysis was performed as described by Lockie (1959) and von Schantz (1980).

Trapping and radio-tracking of foxes. Foxes were trapped with leg snares (von Schantz in press). Subsequent radio-tracking gave information on breeding status and residency of individual foxes.

RESULTS

The field vole population, which was censused throughout this study by L. Hansson (in manus), did not show any significant differences in density between the years (Hansson in manus and Erlinge et al. unpubl.). Nor did the water vole population, which has been studied since 1975, show any marked change in numbers regarding the whole study area (B. Jeppsson pers. comm.). In the following I will, therefore, focus on the changes in the rabbit population and relate these to changes in the fox population.

THE RABBIT POPULATION

The rabbit population increased markedly in density from 1974 to 1976 (Fig. 1). In these years the winters were mild with hardly any snowcover. The winter of 1976/77 was very hard with an unusually thick and long lasting snowcover. During this winter the rabbit population decreased drastically (Fig. 1). In spring 1977 the density was only one third of that in spring 1976 (Table 1).

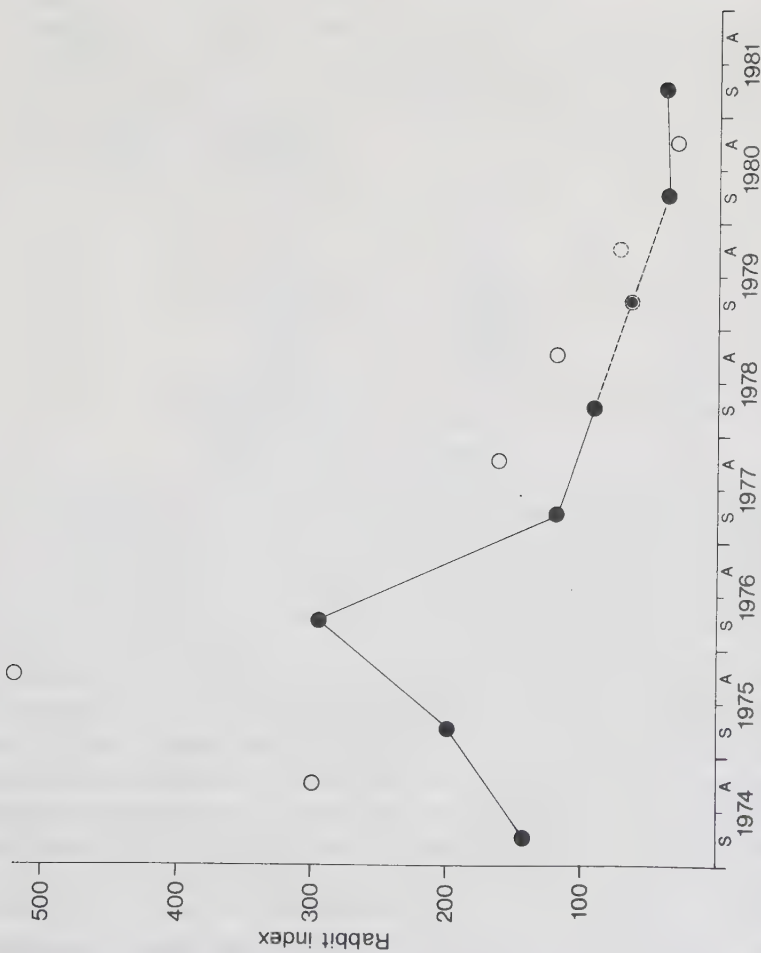


Fig. 1. Indices of rabbit density in the Revinge area from 1974 to 1981. Filled circles denote spring figures and open circles denote autumn figures. The censuses in 1974 and spring 1975 are not based on the same sample plots as from autumn 1975 onwards. To be comparable the index figures from 1974 and spring 1975 are recalculated. The figures in 1979 are intrapolated as no censuses were performed in that year.

Throughout the winter of 1976/77 dead or weak rabbits were frequently observed in the study area. From 1977 onwards the rabbits continued to decrease and they reached their lowest levels in 1980 and 1981 (Fig. 1, Table 1).

TABLE 1

Relative spring densities of rabbits in the Revinge area between 1976 and 1981. The total area of the sample plots for each count of rabbits was approximately 100 hectares (von Schantz and Liberg in press). In the statistical comparisons consecutive years with similar figures (no significant differences) were pooled. $\bar{x}$ = mean number of rabbits counted, N = number of counts.

YEAR	$\bar{x}$	S.D.	N	SIGNIFICANCE OF DIFFERENCE, Mann-Whitney U test
1976	296	76	4	p < 0.01
1977	119	13	5	
1978	92	8	4	p < 0.02
1979	65 ^a		0	
1980	37	6	2	p < 0.01
1981	40	5	5	

^a intrapolated

THE FOXES' FUNCTIONAL RESPONSE TO DIFFERENT RABBIT DENSITIES

The foxes' diet differed before and after the rabbit decrease (Fig. 2). Before the rabbit decrease, i.e. from autumn 1974 to early spring 1977 (when a lot of dead and weak rabbits still were present), lagomorphs (mainly rabbits) were predominant prey (von Schantz 1980). The proportion of lagomorphs (percentage of weight) in the foxes' diet was 86 %, whereas the corresponding figure for voles (field vole and water vole) was only 8 % (Fig. 2). After the rabbit decrease, the prey biomass of lagomorphs in the foxes' diet equalled that of voles (46 % each), as calculated from scats collected from autumn 1977 to winter 1978/79 (Fig. 2). The mean weight of remains of lagomorphs and voles in fox scats was compared for 1974 with intermediate rabbit density, 1975 and 1976 with high rabbit densities, and 1977 with low rabbit density (Table 2). The foxes responded to the increased rabbit density between 1974

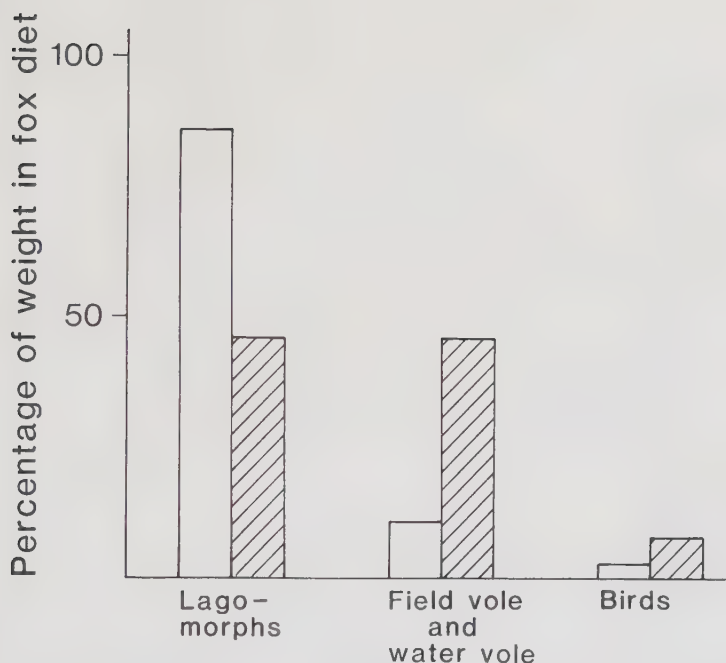


Fig. 2. The diet of the foxes in the study area in years of high and low rabbit density. The analysis is based on 1,028 scats collected from autumn 1974 to spring 1977 with high rabbit density (open bars) and 104 scats collected from autumn 1977 to winter 1978/79 with low rabbit density (hatched bars).

and 1976 by a significant increase in their rabbit consumption and by a significant decrease in their vole consumption. In autumn 1977, i.e. after the rabbit decrease, the foxes fed significantly less on rabbits and more on voles than during the years 1974 to 1976 (Table 2). This occurred without any significant change in numbers in any of the two vole populations.

THE FOXES' NUMERICAL RESPONSE TO CHANGING RABBIT DENSITY

Fig. 3 shows the size of the Revinge fox population in spring and autumn, respectively, from autumn 1974 to spring 1981. The censuses in autumn 1974 and spring 1975 are not based on the same sample plots as from autumn 1975 onwards. Therefore, the figures collected before spring 1975 are not statistically comparable to

TABLE 2

Mean weight of lagomorph and vole (field vole and water vole) remains in fox scats collected in the autumns from 1974 to 1977.

PERIOD	NUMBER OF SCATS	MEAN WEIGHT (g) OF LAGOMORPH REMAINS	S.D.	df	P*	MEAN WEIGHT (g) OF VOLE REMAINS	S.D.	df	P*
Autumn 1974	88	2.47	2.27	198	< 0.001	0.60	0.99	198	< 0.05
Autumn 1975 and 1976	112	3.89	2.96	138	< 0.001	0.33	0.80	138	< 0.001
Autumn 1977	28	0.78	1.05			2.30	2.27		

*t-test

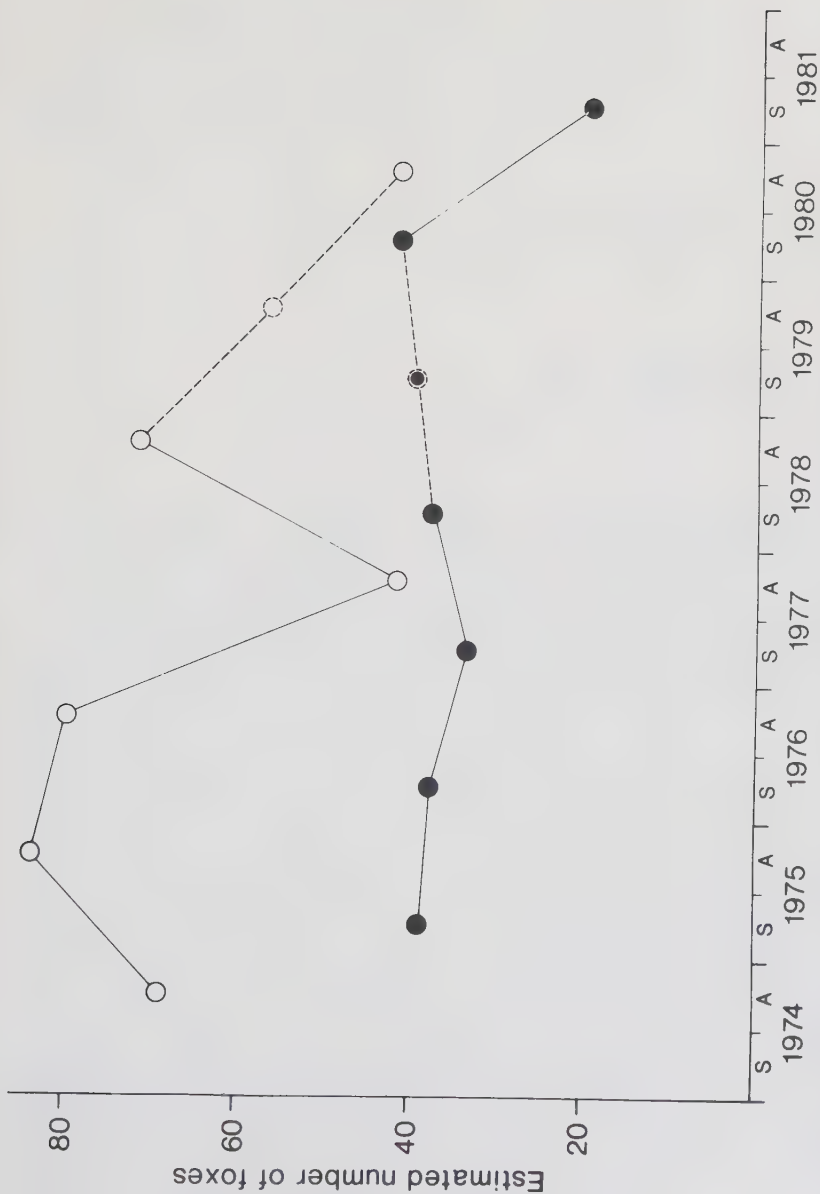


Fig. 3. Estimated number of foxes in the study area based on sample plot counts (von Schantz and Liberg in press). Filled circles denote spring figures and open circles denote autumn figures. The figures in 1979 are intrapolated as no censuses were performed that year.

TABLE 3

Number of foxes counted at the sample plot counts from 1975 to 1981.

	SPRING			AUTUMN		
	$\bar{x}$	S.D.	Number of counts	$\bar{x}$	S.D.	Number of counts
1975				4.00	2.12	5
1976	2.25	1.26	4	3.80	1.10	5
1977	2.00	0.71	5	2.00	0.0	5
1978	2.25	0.50	4	3.40	1.34	5
1979	-	-	0	-	-	0
1980	2.5	0.71	2	2.00	0.71	5
1981	1.2	0.45	5			

those afterwards. Comparing the numbers of foxes counted at each sample plot count (Table 3) shows that the autumn population of foxes after the rabbit decrease (1977, 1978, 1980) was significantly smaller than before the decrease (autumn 1975, 1976) ($p < 0.02$, t-test, two-tailed, $df = 23$). However, spring densities of foxes in 1976 and 1977 (in early spring 1977 there was still many dead or weak rabbits) did not differ significantly from that of 1978, 1980, and 1981 ($p > 0.4$). In 1981, however, the spring population was smaller than in the years before ($p < 0.02$, t-test, two-tailed, $df = 18$).

In 1977 fox reproduction markedly decreased, associated with the rabbit decrease in the winter of 1976/77 (Fig. 4). The number of litters was approximately the same in 1976 and 1977 (15 and 13, respectively) but they were significantly smaller in 1977, on average 3.54 young in 1977 and 5.10 in 1976 ($p < 0.02$, Mann-Whitney U test, two-tailed). The small average litter size in 1977 lead to a smaller total production of fox cubs than in 1976 (Fig. 4). In each of 1978 and 1979 only nine litters were raised (Fig. 4). The mean litter size, however, was higher in these years (1978 $\bar{x} = 5.00$, 1979 $\bar{x} = 5.33$) than in 1977, and so the total number of cubs in 1978 and 1979 equalled that of 1977 (Fig. 4). In 1980, nine dens were occupied by fox litters. However, three of these disappeared at an early stage. Such disappearance of litters

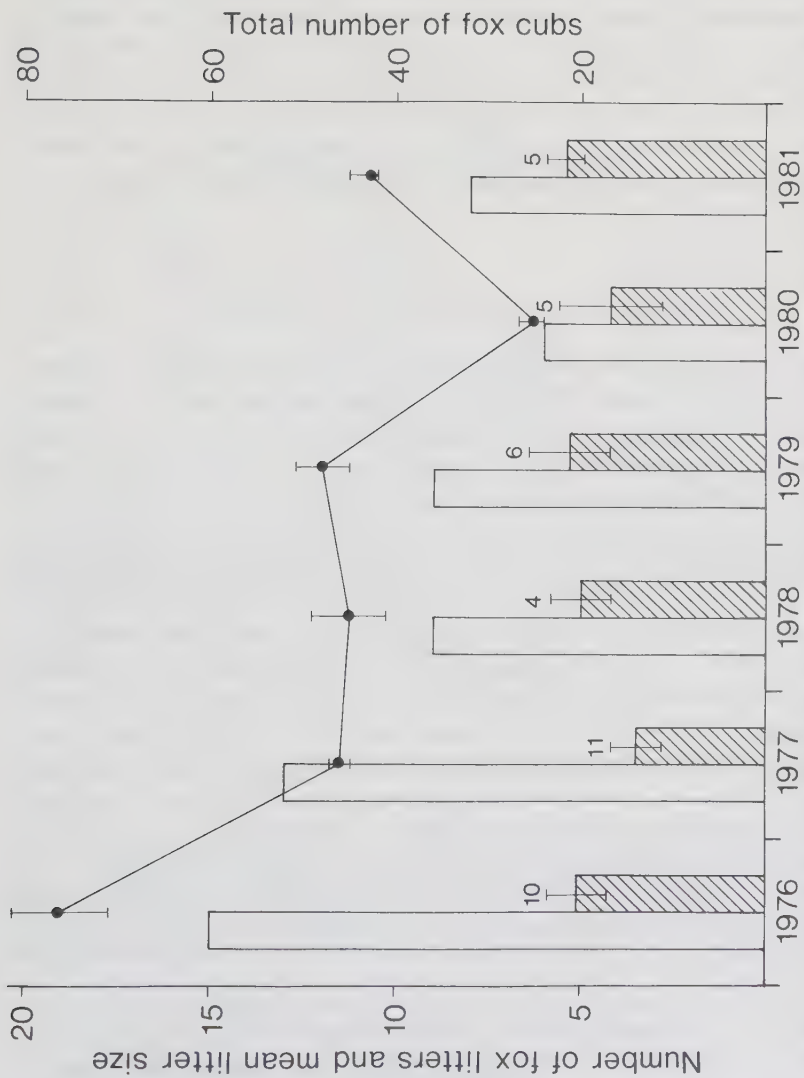


Fig. 4. Number of successful fox litters (open bars), mean litter size (filled circles) within the 95 % confidence level, and estimated total production of fox cubs (hatched bars) within the 95 % confidence level, in the study area between 1976 and 1981. The number of litters was obtained from den counts. The number of litters where the cubs were counted is given above the hatched bars.

was not observed in any other year, and I believe that these three litters were lost. The mean size of the six successful litters in 1980 ($\bar{x}=4.20$) was smaller (but not significantly so) than in 1979 and 1981 (1981 $\bar{x}=5.40$) and the total production of cubs in 1980 was the smallest ever recorded during the study (Fig. 4). The total production of cubs in 1981 (eight litters) was similar to that in 1977 to 1979, and considerably larger than in 1980 (Fig. 4). This increase in the foxes' reproductive success in 1981 as compared to 1980 cannot be correlated with any change in food supply, since the rabbit density was the same these two years (Fig. 1, Table 1).

CHANGES IN THE FOXES' SOCIAL ORGANIZATION

Trapping and subsequent radio-tracking from 1976 to 1980, showed that out of 13 trapped adult foxes (eight females and five males) only one male was itinerant (I recognize a fox as adult once it has reached its first winter). Therefore, it is likely that the majority of the foxes counted in spring were residents in the study area. For six of the eight adult females breeding status could be determined; four of them were non-breeders. Data on spring densities of foxes and the number of fox litters together with information obtained from radio-tracking show that between 1978 and 1980 a great fraction of the adult population consisted of resident non-breeding individuals, the majority of them probably females. Radio-tracking showed that non-breeding females had home ranges within those of the breeding foxes (von Schantz 1981). Radio-tracking at night in April and May, reveals that three non-breeding females visited the litters at most four times out of 125 hours of radio-tracking (one visit per 30 hours of night), whereas one female with cubs visited the litter at least 11 times during 37 hours of radio-tracking (one visit per three hours of night).

In 1976, the cubs in at least two of the 15 litters varied considerably in size and weight, indicating that the litters were mixed. Observations in 1977 on ear-tagged and radio-tagged cubs and subadults from two adjacent litters revealed that also in this year cubs of two different females utilized the same range. This indicates that in 1976 and 1977 more than one female in each group reared cubs. Further, in 1976 and 1977 some of the litters were

situated close to each other. "Litter-mixing" was not observed after 1977 and from 1978 onwards the breeding dens were further apart and more regularly distributed (Table 4) indicating that after 1977 only one female per group raised cubs. CV- and GMASD-values (Brown 1975) show that in 1978 to 1981 the dens were more evenly distributed than in 1976 and 1977 (Table 4).

TABLE 4
Spacing of the foxes' breeding dens.

YEAR	NUMBER OF LITTERS	MEAN DISTANCE TO CLOSEST DEN (km)	S.D.	COEFFICIENT OF VARIANCE ($\frac{S.D.}{\bar{x}} \times 100$)	GMASD*
1976	15	1.12	0.49	44	0.70
1977	13	1.46	0.44	30	0.85
1978	9	1.70	0.24	14	0.97
1979	9	1.96	0.31	16	0.96
1980	6	1.95	0.39	20	0.94
1981	8	2.08	0.33	16	0.96

*The GMASD-value (where one denotes complete regularity and zero denotes complete randomness) is calculated according to the formula of Brown (1975) i.e.:

$$GMASD = \frac{\left(\prod_{i=1}^n d_i^2 \right)^{1/n}}{\left(\frac{\sum_{i=1}^n d_i^2}{n} \right)} \left(\frac{\text{Geometric mean of } d_i^2}{\text{Arithmetic mean of } d_i^2} \right),$$

where n = number of dens, d_i = the distance from the i th den to its closest den.

Censuses in spring gave an estimate of 20 foxes in the area which was considerably lower than in the other years (Fig. 3). In 1981 eight litters were successfully raised, suggesting that this year male-female pairs were the most common social unit and that very few non-breeding individuals were present.

DISCUSSION

Before turning to the details in the dynamics of the fox population, I find it necessary to discuss in more general the evolution of group living.

DO OBTAINED FIELD DATA SUPPORT OR FALSIFY

EXISTING THEORIES ON THE EVOLUTION OF GROUP LIVING?

The benefits for animals living in kinship-groups have been discussed by e.g. Bertram (1978) and Emlen (1978). Bertram (1978) concluded that one advantage of group-living is the greater ability of pack-hunting predators to kill large prey. However, many birds and the red fox hunt solitarily and, therefore, this advantage can explain the evolution of group living for only a few species. For birds, Emlen (1978) listed different potential benefits for breeders and non-breeders due to membership in a group, i.e. for breeders:

- (B1) The non-breeders may help the breeders in care and rearing of their current offspring.
- (B2) The non-breeders could function as an insurance back-up, increasing the probability that the offspring will survive if one of the breeders dies.
- (B3) The experience gained by the non-breeders in rearing young could improve their ability to become successful breeders in the future. On the assumption that the non-breeders are close relatives to the breeders, their future success could increase the inclusive fitness of the original breeders.
- (B4) Competition for space and food between adjacent groups may favour a large group size.

and for non-breeders:

- (H1) Gained experience in caring for young.
- (H2) Increased inclusive fitness by rearing relatives.
- (H3) Access to the resources and security of the group which increases the chance of surviving to the age and status necessary for becoming a breeder.

Emlen (1978) pointed out that point (B1) may be especially important in harsh or unpredictable years, when the parents alone would have difficulty providing food for the young. As to food availability for the foxes, 1980 and 1981 were the most harsh years in this study, since rabbit spring densities were lowest in these years (Fig. 1). In spring 1980 the number of foxes was approximately the same as the years before (Fig. 3). Nine litters were born which indicates that about half the population consisted of non-

-breeders. Yet, in 1980 three litters were lost and the total production of cubs was the lowest ever recorded during the study (Fig. 4). In contrast, in spring 1981 the number of foxes was calculated to be only 20. Eight litters were reared this year, indicating that very few non-breeders were present. Despite the absence of non-breeders and unchanged rabbit density (Fig. 1, Table 1), the foxes produced considerably more cubs in 1981 than in 1980 (Fig. 4). If the non-breeders help the breeders to provide food for the young, we would have expected the opposite result. In addition, radio-tracked non-breeding females visited the litters of their groups only occasionally. Accordingly, in the light of these observations I reject points (B1), (B3), and (H1) above as important selective pressures in the evolution of group living in the red fox.

Point (B2) is supported by the observation that one radio-tracked non-breeding female adopted the litter of the non-breeding female in her group after the death of the latter (von Schantz 1981; see also Macdonald 1979, 1980). Assuming a high mortality rate among breeders during the breeding season this finding also implies that point (H2) could be important. Analogous to point (B2) is the suggestion by e.g. Brown (1974) and Woolfenden and Fitzpatrick (1978) that the acceptance of genetically related non-breeding group members ensures the breeders that the young raised in the territory after their death are related to them. This increases a breeder's inclusive fitness. Points (B4) and (H3) can neither be supported, nor rejected on the basis of available data in this study. Point (H3) is an extension of Selander's (1964) suggestion that habitat saturation might be an important factor in the evolution of group territoriality. If unoccupied territories are scarce, dispersing individuals may have to travel great distances before they can settle. The mortality rate for such dispersers is likely to be high. In such cases, by remaining in the parents' territory as non-breeders the young would increase their survival rate which is beneficial also for the parents. In the red fox I consider habitat saturation a fundamental prerequisite for group living. If there are many unoccupied territories in the surroundings both the breeder and the non-breeder may gain in inclusive fitness by the latter's emigration. Even if it would be beneficial for the breeders to prevent the non-breeder from leaving the group I can see no way for them to do so (cf. Gaston 1978).

Another prerequisite for group living is the fact that the

territory must contain enough resources to support more individuals than the single breeding pair. I have suggested that the evolution of kinship-groups can be induced by a temporary resource surplus within the territories (von Schantz in manus). Theoretically, a territorial and permanently resident animal, like the red fox, living in an interannually fluctuating food environment, should have a constant territory size if the animal's life span is longer than its food cycle. Lindström et al. (in manus) have found that the red fox in central Sweden did not change territory size although its main prey, voles, fluctuated markedly on a four year cycle. An animal following that tactic will not have to fight against neighbours for territorial enlargement each time the food density decreases which would be the case for an animal which adjusts its territory size to current food density. The former's "obstinate strategy" implies that in the "good" years the territory holder will face a situation where the territory contains resources exceeding the owner's need for reproduction and maintenance (von Schantz in manus). In such circumstances the territory holder, i.e. the breeder, should permit some of its offspring to remain as non-breeders in the territory to exploit the super-abundant resources. Besides this advantage, both breeders and non-breeders may benefit in the other ways suggested above (Emlen 1978).

The breeders reared the young successfully without the help of non-breeders in 1981 with low rabbit density (Fig. 4, Fig. 1). From 1976 to 1978 and probably also in 1979 when rabbit densities were considerably higher and when numbers of non-breeders were present, the territories obviously contained more food than needed for the single breeding pairs' own reproduction. These facts support the "resource surplus" view presented above. A similar conclusion was reached by Davies and Houston (1981) who demonstrated that pied wagtails (Motacilla alba) accepted subordinate wagtails in their winter feeding territories on days of high food abundance. By this strategy the territory owner gained help from the subordinate wagtail in territorial defence, which implied that the owner could maintain a fixed territory size. On days of low food abundance the territory owner evicted the subordinate from the territory.

AT DIFFERENT PREY DENSITIES

I shall now turn to the foxes' response to changes in the rabbit population. Let us consider the years 1974 to 1976 when the rabbit population almost doubled (Fig. 1). Yet the density of foxes in spring remained the same whereas the density in autumn increased only slightly (i.e. 16 %) (Fig. 3). In 1976 with high rabbit density more than one female bred per group. Assuming that there were nine groups of foxes in the study area in 1976, as apparently was the case from 1978 onwards, the average group size was 4.2. On the assumption that there was one male in each group (cf. Macdonald 1979) and based on the fact that at least 17 females (two litters were mixed) successfully reared young an average of 2.9 individuals of the group members were breeders; i.e. 68 % of the population. Furthermore, on the basis of these assumptions, each group raised on the average 8.4 cubs. On the other hand, if we assume that there were 15 groups in 1976, then the corresponding figures will be: group size 2.5, average number of breeders per group 2.1 (i.e. 84 % of the population), number of cubs per group 5.1. However, based on different circumstantial evidence (e.g. the distribution of dens, Table 4) I regard the former assumption, i.e. nine groups, as more realistic than the latter. The foxes responded to the increased rabbit density by increased rabbit consumption and decreased vole consumption (Table 2). Breeding foxes in the study area mainly exploited rabbit habitats whereas non-breeders spent most of their time in vole habitats, and it may therefore be that access to rabbits is essential for successful breeding (von Schantz 1981). Thus, instead of increasing group size, the breeders accepted some of the non-breeders to become breeding group members. If so, this explains the foxes' weak numerical response (Fig. 3) to the increase in rabbit density (Fig. 1, 1974-1976). I have suggested (von Schantz in manus) that above a certain prey density it may be profitable for the breeder to allow subordinates to reproduce. On the other hand, a drastic and sudden decrease in the food density can make such a strategy costly for the breeder, for whom the dilemma must be especially great if food fluctuates unpredictably. In spring 1977 the density of rabbits was smaller than in any of the years before (1974-1976) (Fig. 1). However, since dead or weak rabbits occurred all over the area in late winter and early spring the availability of rabbits was obviously

great, which may explain the occurrence of multiple breeding in spring 1977. Later in the breeding season the foxes' reproductive success was negatively affected by the low rabbit density, as seen from the exceptionally small litter sizes (Fig. 4). Mean litter size in 1978, when only one female per group bred, was larger than in 1977 (Fig. 4) in spite of lower rabbit density (Fig. 1). In 1977, the unpredictable (i.e. late) rabbit decrease in combination with the multiple breeding strategy probably caused the reduced breeding success of the foxes. In 1977-1980 the spring densities of foxes remained the same as the years before (Fig. 3), but from autumn 1977 the foxes began to consume considerable amounts of voles, a resource that had been only weakly exploited before (Fig. 2). This may be attributed to the increased proportion of non-breeding group members (as computed from spring densities of foxes and number of litters) who, in contrast to the breeders, mainly hunted for voles (von Schantz 1981). By this strategy the non-breeders avoided competition from the breeders in their group and thereby reduced the cost to the breeders for accepting the presence of non-breeders (von Schantz 1981). As the foxes' breeding success was poor (Fig. 4) in 1980, when rabbits were few (Fig. 1) and non-breeders still present, this strategy was apparently not sufficient in reducing the cost to the breeder. That the breeders alone could have bred successfully at this prey density is suggested by the foxes' successful breeding in 1981 (Fig. 4) when hardly any non-breeders were present. Why then did not the breeders evict the non-breeding group members in 1980, thereby avoiding competition from them? There can be at least two reasons for this, of which none can be rejected on the basis of this study, namely:

- (1) The breeders could not predict the low food density.
- (2) A parent who has only enough food to keep one of two offspring alive should prefer to invest in that offspring which is going to need less investment in the future (Dawkins and Carlisle 1976). Since the non-breeding group members presumably were the breeders' adult offspring it could pay the breeders more by continue to invest in the non-breeders (i.e. allowing them to exploit the restricted resources in the territory) rather than to invest heavily in a new litter whose future life expectancy would be low anyhow.

In conclusion: Group living of red foxes in southern Sweden seems to be a consequence of a resource surplus which probably is induced by the territory holder's reluctance to adjust territory size according to fluctuations in food abundance. By keeping a constantly sized territory the owners do not have to struggle for territorial enlargement when food density decreases. Such a strategy can become stable by the breeders' acceptance of adult offspring exploiting the super-abundant food resources in the territory during the "good" years (von Schantz in manus). Furthermore, by adopting this strategy and on the assumption that the habitat is saturated (Selander 1964) the breeding foxes increase the probability that: (1) the territory is inherited by relatives, (2) the survival rate of the non-breeding group members, which probably are the breeders' adult offspring, increases, (3) on their death their current offspring will be adopted by the non-breeders, and (4) they may gain help from the non-breeders in territorial defence. In addition, the non-breeding group members increase the probability that: (1) they will survive to the age and status necessary for achieving breeding status, and (2) that they will inherit a territory and, thus, breeding status.

I reject the helper effect, i.e. the helpers aid to the breeders in their reproductive efforts, as an important selective force in the evolution of group living in the red fox. I do not deny the fact that "helpers" may help in the red fox and other species in order to increase their inclusive fitness. However, I question its significance in the evolution of group living (see also references cited by Emlen 1978). This study suggests that helping at the nest is a consequence of group living rather than the cause of it.

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